Scientific Papers

Natural History Museum
The University of Kansas

31 March 2005 Number 38:1–27

Systematics of the *Bufo coccifer* Complex (Anura: Bufonidae) of Mesoamerica

By

MCZ
LIBRARY
JUL 23

Joseph R. Mendelson III[1], Becky L. Williams[2], Christopher A. Sheil[3],
and Daniel G. Mulcahy[4]

[1] *Department of Herpetology, Zoo Atlanta, 800 Cherokee Ave SE, Atlanta, GA 30315*
[2] *Department of Integrative Biology, University of California, Berkeley, CA 94720-3140*
[3] *Department of Biology, John Carroll University, University Heights, OH 44118*
[4] *Department of Biology, Utah State University, Logan, UT 84322-5305*

CONTENTS

ABSTRACT 2
RESUMEN 2
INTRODUCTION 2
  Acknowledgments 5
MATERIALS AND METHODS 5
  Morphological Data 5
  Molecular Data 6
ACCOUNTS OF SPECIES 6
  Bufo coccifer 6
  Bufo cycladen 11
  Bufo ibarrai 13
  Bufo pisinnus 15
  Bufo porteri 17
  Bufo signifer 20
MORPHOMETRIC ANALYSES 22
MOLECULAR ANALYSES 23
LITERATURE CITED 24
APPENDIX 26

Ernst Mayr Library
Museum of Comparative Zoology
Harvard University

ISSN No. 1094-0782

ABSTRACT Many populations of toads occurring between west-central Mexico and Panama have been referred to *Bufo coccifer* Cope, 1866. While the taxonomic status of these populations has been questioned for many decades, a thorough review of the *B. coccifer* complex never has been presented. Based on evidence from external morphology and a partial molecular data-set, we conclude that this complex consists minimally of six species. Herein, we recognize *B. coccifer* Cope, 1866, *B. cycladen* Lynch and Smith, 1966, and *B. ibarrai* Stuart, 1954, and describe three new species.

Key Words: Bufonidae; *Bufo coccifer, Bufo cycladen, Bufo ibarrai, Bufo pisinnus, Bufo porteri, Bufo signifer;* Mesoamerica; taxonomy.

RESUMEN Muchas poblaciones de sapos que se encuentran entre el oeste-central de México y Panama han sido referidas como *Bufo coccifer* Cope 1866. Aunque el estado taxonómico de estas poblaciones ha sido cuestionado por muchas decadas, nunca se ha presentado una revisión completa del complejo *B. coccifer.* En base a evidencia de morfología external y una base de datos moleculares parcial, concluimos que este complejo consiste de al menos seis especies. En este trabajo, reconocèmos *B. coccifer* Cope, 1866, *B. cycladen* Lynch and Smith, 1966, y *B. ibarrai* Stuart, 1954, y describimos tres especies nuevas.

Palabras Clave: Bufonidae; *Bufo coccifer, Bufo cycladen, Bufo ibarrai, Bufo pisinnus, Bufo porteri, Bufo signifer;* Mesoamérica; taxonomía.

INTRODUCTION

The taxon *Bufo coccifer* Cope, 1866 currently is applied to toads that are distributed allopatrically in five regions of Mesoamerica (Fig. 1): (1) the Tepalcatepec Valley, Michoacán, Mexico; (2) the Pacific slope of the Sierra Madre del Sur in Guerrero, Mexico; (3) the southern side of the Isthmus of Tehuantepec, Oaxaca, Mexico; (4) nearly the entire Pacific versant from northwestern Guatemala to northwestern Costa Rica; and (5) western Panama. Additional records exist from the Atlantic versants of Honduras and Nicaragua. The distribution of these populations approximately matches the distribution of low elevation tropical dry forest (Rzedowski, 1994; Campbell, 1999) in these regions. However, the population on the Pacific slope of the Sierra Madre del Sur is an exception to this generality; these toads are found at moderate elevations (ca. 1000 m) in relatively wet pine-oak forest. (See Campbell and Duellman, 2000, for habitat description.) Other records from more mesic, upland habitats include the mountains of central Honduras (McCranie and Wilson, 2002). An additional species, *B. ibarrai* Stuart, frequently has been assigned to the *Bufo coccifer* Group (e.g., Frost, 1985). The taxonomic status and distribution of *B. ibarrai* was reviewed by Mendelson (2001); this species occurs primarily in upland pine-oak habitats in Guatemala and is reported here for the first time in an adjacent region of Honduras.

With reference to the broad distribution of *Bufo coccifer*, it has been suggested many times that these various populations likely are not conspecific (Stuart, 1954a, 1963; Duellman, 1960; Porter, 1963, 1965; Zweifel, 1965; McDiarmid and Foster, 1981; Mendelson, 2001; McCranie and Wilson, 2002). Dunn and Stuart (1951) commented on the status of the type locality for *B. coccifer* ("Arriba" Costa Rica: Cope, 1866:130) and suggested that the holotype likely originated from somewhere on the Meseta Central of Costa Rica; this referral was supported by Savage (1974). Porter (1963) provided a range map and general diagnosis of *B. coccifer.* Porter (1965) discussed the distribution of the species in more detail, observing that the populations in Michoacán, Mexico, and Oaxaca, Mexico, evidently are allopatric—with a hiatus of approximately 140 km between records from Oaxaca, Mexico, and records from southeastern Guatemala. Stuart (1954a:20) referred to "a chain of *Bufo coccifer*-like toads" distributed through the subhumid habitats of Central America, and specifically noted undescribed species in central Guatemala, and another in Guerrero and the Isthmus of Tehuantepec region of Mexico. Stuart (1954b) subsequently described the populations in the upland pine-oak zone of Guatemala as *B. ibarrai.* Lynch and Fugler (1965) reported *B. ibarrai* from Honduras. Subsequently, the taxon has had a long period of uncertain status, typically being confused with *B. coccifer* (e.g., comments by J. A. Campbell *in* Frost, 1985:41). Meyer and Wilson (1971) placed *B. ibarrai* in the synonymy of *B. coccifer.* However, Mendelson (2001) recognized *B. ibarrai* as a distinct species, described the tadpole, and provided a new diagnosis and range map of records from Guatemala; also, he suggested that the species may be endemic to Guatemala. Based on examination of specimens from Honduras, McCranie and Wilson (2002) suggested that *B. ibarrai* does not occur in that country. Lynch and Smith (1966) referred all populations in Mexico to the new taxon *Bufo cycladen* and cited differences in the advertisement call (fide Porter, 1965) and ecology of the Mexican and Central American populations. However, the morphology of this taxon was

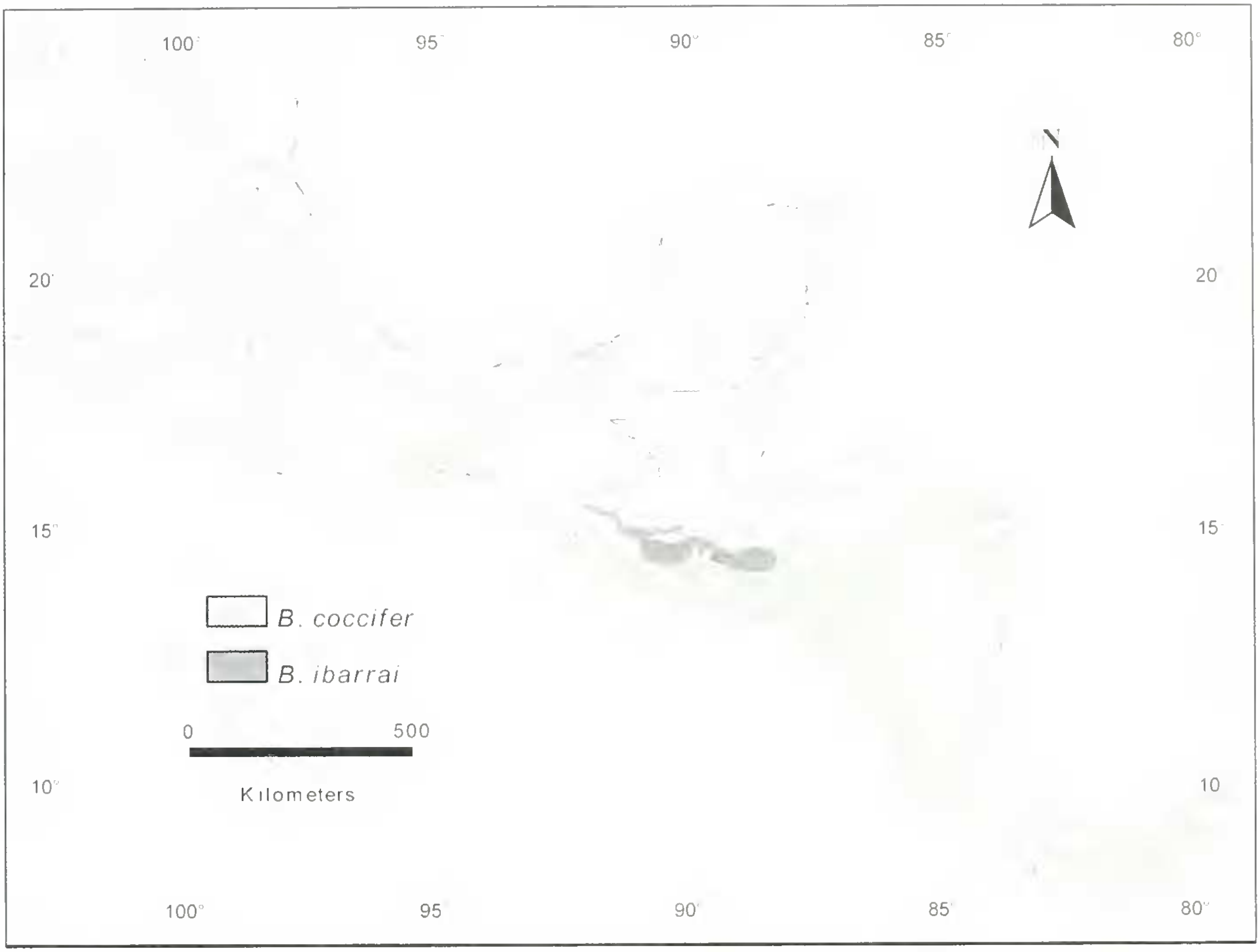

Fig. 1. A map of Mesoamerica, showing the generalized distributions of toads referred to *Bufo coccifer* sensu lato, and of *B. ibarrai* (as recognized herein).

diagnosed poorly, with respect to *B. ibarrai* (see Mendelson, 2001) and other populations referable to *B. coccifer* (Porter, 1967). Porter (1967) criticized Lynch and Smith (1966) for not supporting their claims of morphological differences among the populations and also claimed that there are no real ecological differences among the populations considered; Porter proposed this taxon to be a *nomen dubium*. The taxonomic confusion surrounding *B. cycladen* is evident in the fact that the taxon appears on some recent checklists (e.g., Frost, 1985), but not on others (e.g., Flores-Villela, 1993; Campbell, 1999).

Several authors have described the male advertisement calls from various areas. Porter (1964, 1965) described the advertisement calls of *B. coccifer* from the Tehuantepec region of Oaxaca, Mexico, in addition to those of toads he referred to *B. coccifer* recorded in Guerrero, Mexico, and several populations in Central America (El Salvador, Honduras, Nicaragua, and Costa Rica; Porter, 1965). The various descriptions and comparisons of advertisement calls presented by Porter (e.g., 1964, 1965) are difficult to interpret because he provided no voucher numbers for recorded specimens, and the detail of his locality information is inconsistent. When tracking down specific locality data provided by K. R. Porter, we found it useful to refer to recording station descriptions presented in his original, unpublished dissertation (Porter, 1962:table 1). Zweifel (1965) first reported the presence of toads he referred to *B. coccifer* in Panama and demonstrated that the advertisement call of this population differed from those of both the Mexican (= Isthmus of Tehuantepec region of Oaxaca) and other Central American recordings that were published by Porter (1964). McDiarmid and Foster (1981) described additional advertisement calls recorded in Costa Rica, and compared them to those reported from Mexico and Central America (Porter, 1965) and from Panama (Zwiefel, 1965); there are substantial differences in pulse

Table 1. Comparison of ranges or means of calls of the *Bufo coccifer* complex from different populations. The identity of the toads recorded from Honduras (Porter, 1965) are unknown because the original paper provides neither reference to voucher specimens nor a detailed locality description; there are at least three species in this group in Honduras.

Location	No. individuals recorded	Duration (second)	Frequency (Hertz)	Pulse Rate (per second)	Source	Species identity
Mexico: Guerrero	1 (6 calls)	mean = 5.7	mean = 2800	mean = 120	Porter, 1965	*B. cycladen*
Mexico: Oaxaca	18	1.4–6.4	2800–3350	97–115	Porter, 1964, 1965	*B. coccifer*
El Salvador	14	3.0–16.3	2200–2700	80–101	Porter, 1965	*B. coccifer*
Guatemala	7	4.2–5.8	1650–1800	48–61	Porter, 1966	*B. ibarrai*
Honduras	2	5.3–8.8	2200–2500	80–96	Porter, 1965	unknown
Nicaragua	4	6.2–10.9	2300–2400	91–100	Porter, 1965	*B. coccifer*
Costa Rica	4	1.5–10.0	2300	90–95	Porter, 1965	*B. coccifer*
Costa Rica	1	1.2–5.7	2231–2539	90–105	McDiarmid & Foster, 1981	*B. coccifer*
Panama	1	8.0–17.0	2100–2600	66	Zweifel, 1965	*B. signifer*

rates and dominant frequencies among these samples. Porter (1966) described the advertisement call of *B. ibarrai*. The data reported by Porter, Zweifel, and McDiarmid and Foster are presented in Table 1 and summarized in Figure 2. We are unaware of any recordings of populations of *B.* cf. *coccifer* from Guatemala or Michoacán, Mexico.

The calls of male toads from the Sierra Madre del Sur of Guerrero and the Tehuantepec region of Oaxaca have higher dominant frequencies than calls of all other samples. The call of the toad in Guerrero also has a higher pulse rate than all other reported calls. Note, however, that the data from Guerrero are based on a recording of six separate calls by the same individual. These data were used, in part, by Lynch and Smith (1966) to justify recognition of all Mexican populations (including populations in Michoacán, Guerrero, and Oaxaca) as a species (*B. cycladen*) distinct

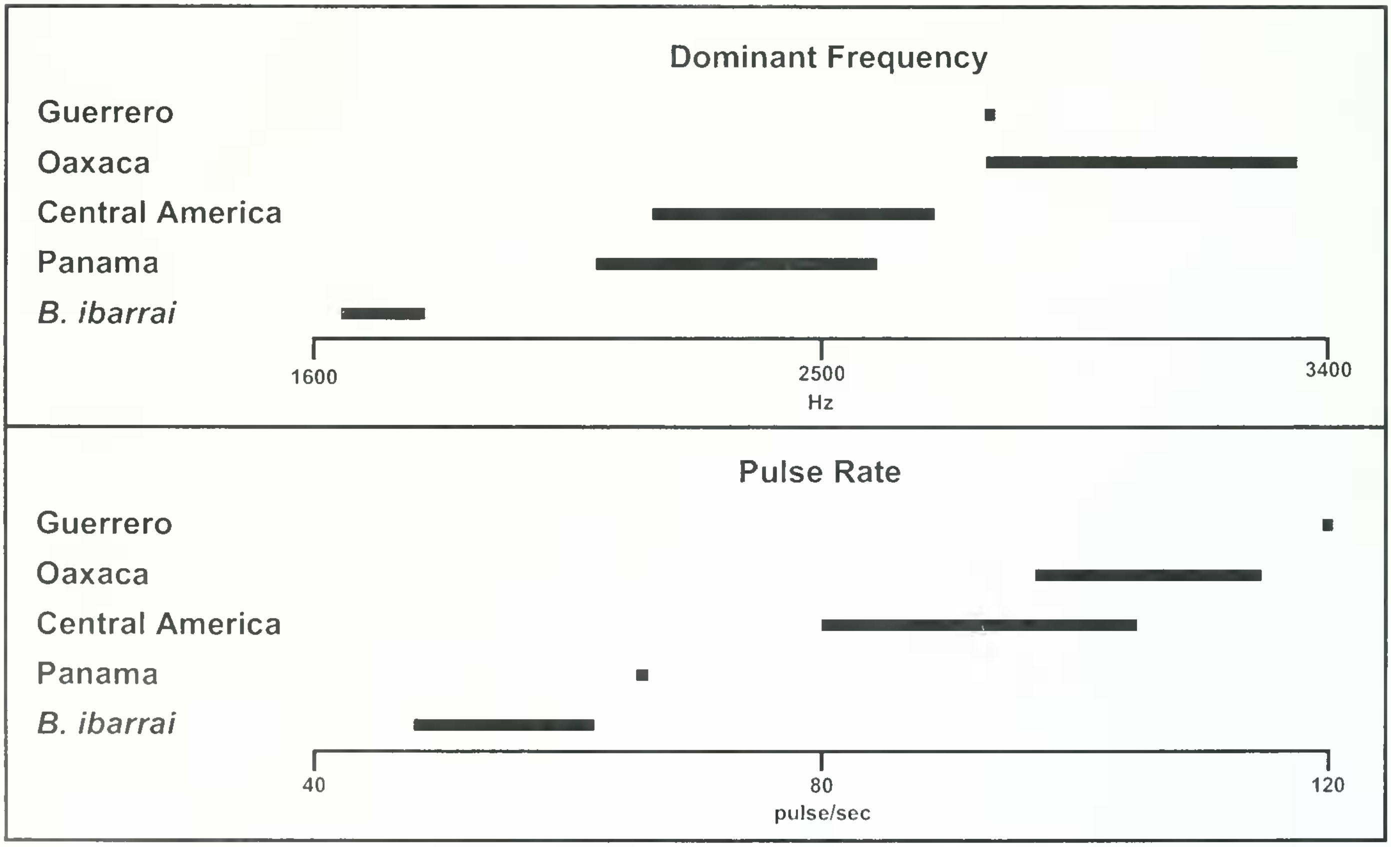

Fig. 2. Graphical representation of frequencies and pulse rates of advertisement calls from toads of the *Bufo coccifer* complex from different regions of Mesoamerica; information shown here are a graphical representation of data presented in Table 1. Data from "Central America" here includes range of values representing samples from El Salvador, Nicaragua, and Costa Rica.

from *B. coccifer* in Central America. A call described by Zweifel (1965) from Panama differs dramatically from all others by having a much lower pulse rate. The relationship between the calls from Oaxaca and Central America is interesting in that they have distinctly different ranges of dominant frequencies and somewhat different (but overlapping) ranges of pulse rates. However, we note that the Central America data do not include recordings from Guatemala—the closest geographic region southeast of the Oaxacan population. Recordings from Guatemala may diminish the apparent distinction between the advertisement calls from the Tehuantepec region of Oaxaca and Central America. Porter (1966) described the call of *B. ibarrai* from Guatemala; this species differs from all other populations in the *B. coccifer* complex by having a very low frequency and pulse rate (Table 1).

In their description of *Bufo cycladen*, Lynch and Smith (1966) placed great diagnostic importance on variation in calls between Mexican and Central American populations. We note that their summary of calls from Mexico was a composite of data from both Guerrero and the Tehuantepec region of Oaxaca (data published by Porter, 1964, 1965; Table 1). We have concluded that these toads from Guerrero are not conspecific with those from Oaxaca (discussed below). Gergus et al. (1997) described call variation among toads of the *B. microscaphus* complex; they reported wide variation in some parameters and an overall pattern of apparent plesiomorphic similarity among allopatric species. There is no reason to expect drastic differences in mate-recognition systems among allopatric members of a complex of closely related anurans with similar natural histories (Gergus et al., 1997). Nevertheless, there are apparent differences in the advertisement calls of toads of the *B. coccifer* complex that suggest diagnostic differences in the mate-recognition systems of these allopatric populations.

All previous workers (above citations) have expressed frustration in delimiting species in this complex, which is characterized by advertisement calls that vary among populations and subtle morphological differences. An expressed or implied consensus of these authors is that a thorough revision of the *Bufo coccifer* complex is long overdue. In this paper we use data from external morphology and male advertisement calls (previously published) to delimit species boundaries among samples referable to the widespread taxon *B. coccifer*. We also present a preliminary assessment of phylogenetic relationships among the species in the group, based on mtDNA data from several of the species.

ACKNOWLEDGMENTS

We are grateful to the following individuals for providing assistance in the field, laboratory, and library: W. Duellman, S. Gotte, K. Lips, M. Acevedo, E. Greenbaum, J. R. McCranie, J. Malone, D. Laurencio, M. Sasa-Marin, M. Ryan, M. Forstner, T. Reeder, J. Campbell, E. Smith, C. Franklin, and R. Gutberlet. Adele Cutler provided statistical advice and assistance. Michelle Koo graciously provided access and assistance with mapping software at the California Academy of Sciences. We benefited greatly from memories, observations, and notes drawn from the considerable field experiences of J. Campbell, C. Myers, J. Savage, W. Duellman, and R. Zweifel. Permission and help with photographs was provided by M. Sasa-Marin, R. Zweifel, and J. Simmons. Loans of critical specimens, for extended periods of time, are gratefully acknowledged from the curators and collection managers of the following institutions: AMNH, CAS, FMNH, TCWC, UTA, TNHC, ANSP, UIMNH, USNM, KU, UMMZ, MVZ, LACM, and LSUMZ. Some of the fieldwork for this project was supported by funds from The National Geographic Society and this research was conducted in direct association with The Research Analysis Network for Neotropical Amphibians (RANA; NSF-DEB 0130273). Comments on the manuscript were provided by the students and faculty of the USU Herpetology Group, L. Trueb, J. Pramuk, and W, Duellman. Additional help and favors were provided by J. Meik and G. Schneider.

MATERIAL AND METHODS

General terminology and measurements are those of Mendelson (1997). Adult males were identified by the presence of vocal slits and nuptial excrescences; large individuals lacking these characters were presumed to be adult females. If sex could not be determined externally, it was verified by direct observation of the gonads. Foot-webbing formulae follow the system of Savage and Heyer (1967), as modified by Myers and Duellman (1982) and Savage and Heyer (1997). The general format of the descriptions and diagnoses is slightly modified from that of Mendelson (2001). Museum codes are those proposed by Leviton et al. (1985). We follow Tyler et al. (2001) in our usage of the term "parotoid gland." Data from advertisement calls were taken from the literature (referenced below).

MORPHOMETRIC DATA

The following measurements were taken from adult specimens: snout–vent length (SVL); head length (HL); head width (HW); tibia length (TIB); foot length (FL); width of tympanum (TYM); length of parotoid gland (PARL); maximum width of parotoid gland (PARW); and length of supratympanic crest (SPTYM). These variables represent repeatable morphological landmarks and were measured with digital calipers and rounded to the nearest 0.1 mm. Because of the paucity of large series of females from many localities, all morphometric analyses are based only on adult males. Many of the data for *Bufo ibarrai* are the same presented by Mendelson (2001), but supplemented with additional material from both Guatemala and Honduras.

We conducted a Principal Components Analysis (PCA) using the covariance matrix on log-transformed morphometric measurements from 324 adult male toads; this data-set included specimens representing all species and geographic regions of the distribution of the *Bufo coccifer* complex. We also performed a PCA on the residuals of the latter seven variables derived from a regression analysis (using SVL as the independent variable). This type of PCA removes the effect of size, and displays general variation in shape and proportion among the specimens (Good and Wake, 1992). We performed a Linear Discriminant Function Analysis (LDA) on the same data-set, and used residuals of variables regressed on SVL and log-transformed SVL. In this analysis, a priori groupings corresponded to the species recognized in this paper (Accounts of Species, below). Statistical analyses were performed using SAS and Minitab software.

Molecular Data

We conducted molecular analyses on all available samples, which included five specimens of *Bufo coccifer* (4 from Central America, 1 from Guerrero, Mexico) and two specimens of *B. ibarrai*. Additionally, one specimen of each of the following species was included as outgroup taxa: *B. coniferus*, *B. valliceps*, and *B. marinus*. The selection of these outgroup taxa was based on preliminary analyses of a data set containing approximately 25 species of Central American bufonids (Mendelson and Mulcahy, in prep.). Sections of the mitochondrial genes cytochrome-b (cyt-b) and 16S were used in the molecular analyses. Isolation and PCR amplification of the mitochondrial DNA (mtDNA) genes were performed exactly as described in Mulcahy and Mendelson (2000), which includes primer information and amplification profiles. Products from the PCR were amplified and sequenced in both directions using BigDye™ Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems Part No. 4303152); we used the same PCR primers and standard sequence-reaction profile on a Perkin Elmer GeneAmp 2400 cycle sequencer. Cleaned sequences were then run on an ABI 377 automated sequencer by DGM at the Biology Department at Utah State University. Sequence comparisons and alignment were conducted with Sequencher 3.1.

Phylogenetic analyses of the mtDNA sequences were conducted using PAUP* 4.0b8a (Swofford, 2002). A partition-homogeneity test of 100 replicates was implemented in PAUP (using default parsimony settings, with the exception of addition-sequence being random with 100 replicates) between cyt-b and 16S gene regions to determine whether or not the two genes yielded conflicting results. Maximum-parsimony analyses (MP) were performed on each gene separately and both combined. The program Modeltest (Posada and Crandall, 1998) was used to evaluate the best Maximum-likelihood model, using the Hierarchical Likelihood Ratio Tests (hLRTs) criterion. A Maximum-likelihood (ML) analysis was then conducted using the model and settings based on the hLRTs results. Because of the limited number of taxa in the phylogenetic analyses, an exhaustive search was possible, and used in the MP analysis, while the ML analysis required a heuristic search algorithm. Gaps were treated as "missing data," with characters-state optimization set at ACCTRAN. Branch support was assessed by nonparametric bootstrap analyses using 1000 replicates of full heuristic searches, with 100 random additions at each replicate, under MP and 100 replicates of full heuristic searches, with 10 random additions under the ML criteria. Decay indices (Bremer, 1994) were also measured under the parsimony analysis using the program TreeRot (Sorenson, 1996).

ACCOUNTS OF SPECIES

We used data from advertisement calls, morphometry, external morphology, and DNA sequences to examine variation among samples of the *Bufo coccifer* complex. These data are consistent with the "chain of *Bufo coccifer*–like toads" distributed through the subhumid habitats of Central America that Stuart (1954a) envisioned. Evaluation of our data with respect to the Evolutionary Species Concept (sensu Wiley, 1978; Frost and Hillis, 1990) supports recognition of six species in this complex. Our proposed taxonomy reflects the sentiments of the many authors (e.g., Stuart, 1954a, 1963; Duellman, 1960; Porter, 1963, 1965; Zweifel, 1965; McDiarmid and Foster, 1981; Mendelson, 2001; McCranie and Wilson, 2002) who have dealt with these toads during the last five decades. We provide species accounts and diagnoses for *B. coccifer*, *B. cycladen*, and *B. ibarrai*, and describe three new species from this complex; photographs of these species in life are presented in Figure 3.

Bufo coccifer Cope
Figs. 3–5

Bufo coccifer Cope, 1866:130. Holotype: USNM 6490. Type locality: "Arriba" Costa Rica.

Bufo coccifer—Dunn and Emlen, 1932; Kellogg, 1932; Hartweg and Oliver, 1940; Dunn and Stuart, 1951; Smith and Taylor, 1948 [in part]; Mertens, 1952; Taylor, 1952; Stuart, 1954b; Rand, 1957; Duellman, 1960; Porter, 1963 [in part]; Stuart, 1963; Porter, 1964; Porter, 1965 [in part];

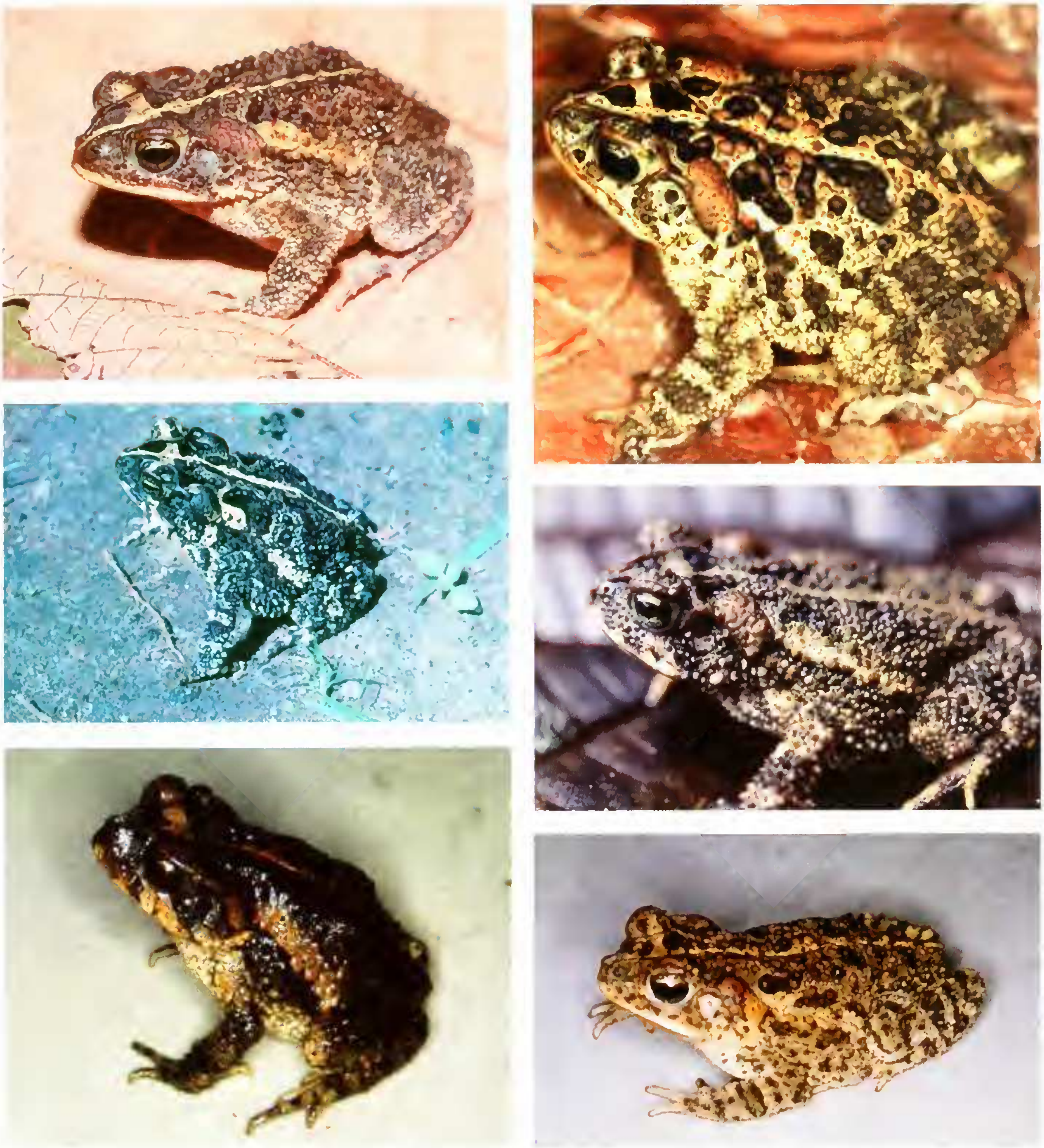

Fig. 3. Species of the *Bufo coccifer* complex in life, clockwise from upper left: *B. coccifer* from Santa Rosa, Costa Rica (adult male; photograph by Andrea Bernecker); *B. cycladen* from Guerrero, Mexico (adult male, UTA-JRM 4607; photograph by J. R. Mendelson); *B. ibarrai* from Baja Verapaz, Guatemala (female, KU 186304; photograph by J. A. Campbell); *B. pisinnus* from Michoacán, Mexico (adult male, from UMMZ series; photograph by W. E. Duellman); *B. porteri* from Francisco Morazán, Honduras (subadult female, KU 103220; photograph by W. E. Duellman); *B. signifer* (adult female, AMNH 69625; photograph by R. G. Zweifel).

Lynch and Fugler, 1965; Porter and Porter, 1967; Meyer and Wilson, 1971 [in part]; Villa, 1972; Savage, 1974; McDiarmid and Foster, 1981; Villa, 1983; Frost, 1985 [in part]; Savage and Villa, 1986; Villa et al., 1988; [in part]; Campbell and Vannini, 1989 [in part]; Flores-Villela, 1993 [in part]; Campbell, 1999 [in part]; Köhler, 1999; Mendelson, 2001; Frost, 2003 [in part]; McCranie and Wilson, 2002 [in part]; Savage, 2002.

Bufo cycladen— Lynch and Smith, 1966 [in part, for reference to specimens from Tehuantepec region of Oaxaca, Mexico]; Frost, 1985 [in part]; Frost, 2003 [in part].

Bufo ibarrai—Lynch and Fugler, 1965 [in part].

Bufo valliceps microtis— Werner, 1896 (synonymy by Mendelson, 2001).

Diagnosis.—A medium to large species of *Bufo* (males to 62 mm SVL; females to 82 mm SVL) having the following combination of characters: (1) tympanum evident externally, about 35–45% diameter of orbit in males and females; (2) canthal, supraorbital, supratympanic, postorbital, preorbital, pretympanic, parietal, and supralabial crests present; (3) cranial crests well developed, robust, except parietal may be thin, low, or absent in some specimens; (4) tibia short, about 35% SVL; (5) feet short, about 35% SVL; (6) dorsal tubercles small to medium sized, elevated, rounded, scattered relatively sparsely on middorsal, dorsolateral, and lateral regions of body becoming more densely arranged and distinctly spinose laterally in specimens from most regions; (7) ventral tubercles granular, smooth, or with spinose apices; (8) lateral descending row of enlarged tubercles absent; (9) skin texture not sexually dimorphic; (10) vocal slit unilateral in male; (11) *m. interhyoideus* poorly differentiated from *m. intermandibularis,* but differentiated posteriorly forming a large, unilobed vocal sac with heavy black pigmentation; (12) snout rounded in lateral profile, pointed in dorsal aspect; (13) parotoid glands round to ovoid and large, about

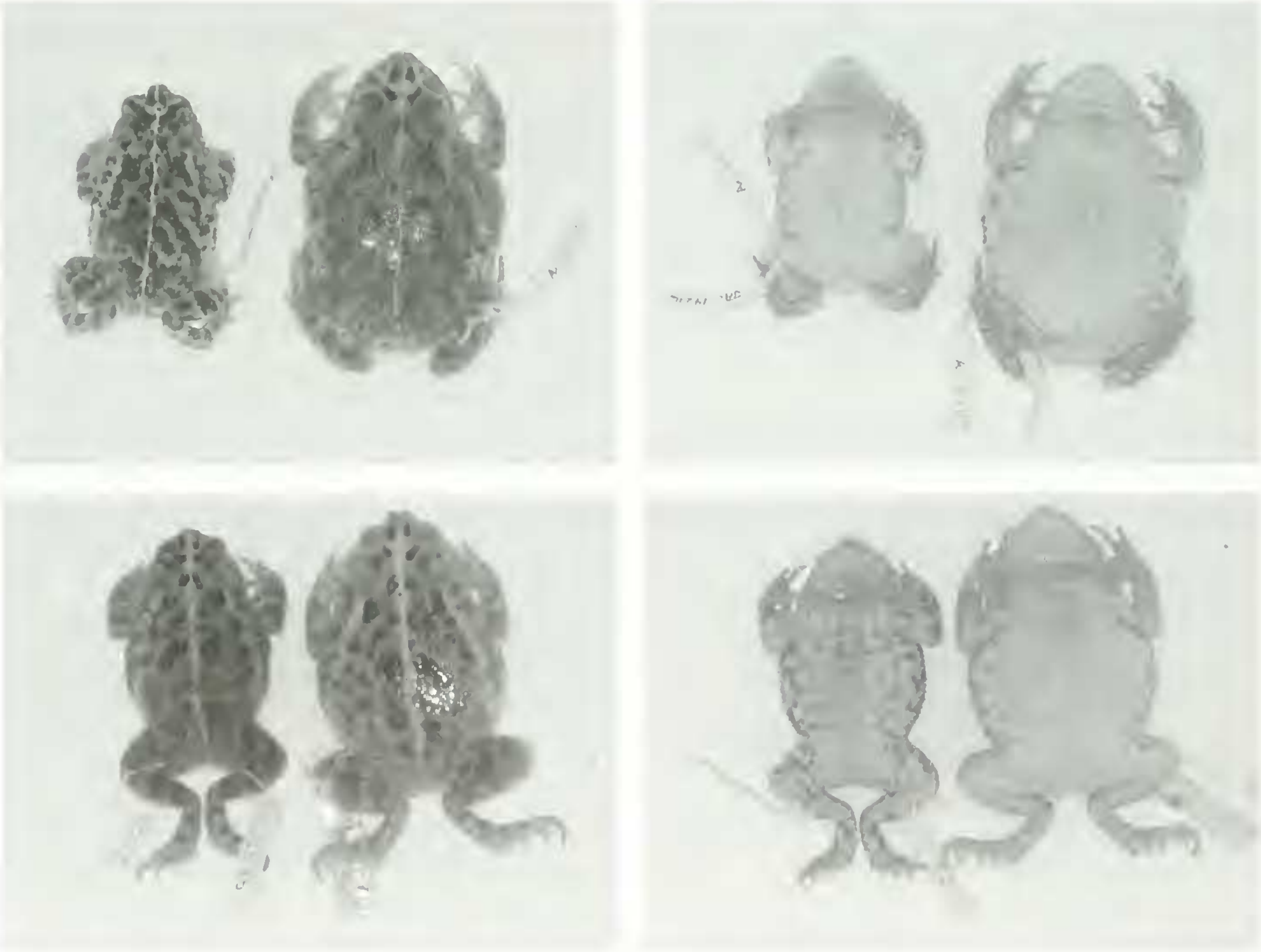

Fig. 4. Dorsal and ventral aspects of representative adult specimens of *Bufo coccifer* from Retalhuleu, Guatemala (male, left: UTA A-25821, SVL = 57.0 mm; female, right: UTA A-29025, SVL = 75.0 mm) and *B. cycladen* from Guerrero, Mexico (male, left: UMMZ 115357 [WED 9275], SVL = 53.8 mm; female, right: UMMZ 119270 [WED 13425], SVL = 61.4 mm).

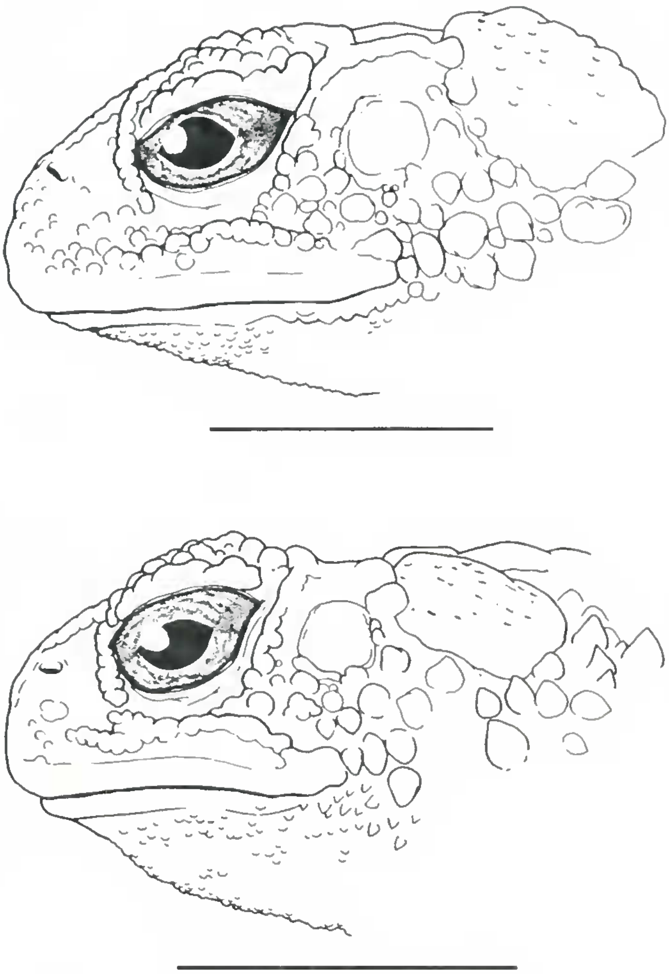

Fig. 5. Lateral aspects of the heads of adult male specimens of *Bufo coccifer* (upper: KU 65400) and *B. cycladen* (lower: KU 97434). Scale bars = 1 cm.

1.0–1.5 times size of eyelid; (14) skin between cranial crests on top of head with few to many scattered, low, rounded tubercles; (15) ventral coloration whitish cream, sometimes with some degree of diffuse dark pigmentation, sometimes in the form of diffuse punctuations.

Specimens referable to *Bufo coccifer* vary considerably in size, shape, coloration, skin texture, and parameters of the advertisement call across the range of the species. *Bufo coccifer* differs from *B. cycladen* by: being larger (males of *B. cycladen* to 54 mm SVL, females to 62 mm); having dorsal tubercles that are relatively small and scattered about the dorsal surfaces, rounded on dorsum, becoming spinose laterally in most specimens (tubercles large, elevated, and densely arranged in *B. cycladen*, rounded dorsally, becoming very spinose laterally); ventral tubercles that are smoothly granular or with small, spinose apices (ventral tubercles in *B. cycladen* with distinct, large spinose apices); relatively well developed parietal crests that rarely are absent (parietal crest weakly developed in *B. cycladen*, sometimes absent); and an advertisement call with a lower pulse rate (Table 1; Fig. 2). *Bufo coccifer* can be distinguished from *B. pisinnus* by: being larger (males of *B. pisinnus* to 51 mm SVL, females to 62 mm); and having skin tubercles that are overall larger (all tubercles minute in *B. pisinnus*). *Bufo coccifer* may be distinguished from *B. signifer* by having: no, or few, relatively indistinct dark brown markings on the venter (that of *B. signifer* boldly marked with a marbled pattern); relatively thicker and higher cranial crests (all crests relatively low and thin in *B. signifer*); and an advertisement call with a higher frequency and pulse rate (Table 1; Fig. 2). *Bufo coccifer* differs from *B. ibarrai* by: being smaller (males of *B. ibarrai* to 82 mm SVL, females to 94 mm); having rounded to subovoid parotoid glands about 1.0–1.5 times size of eyelid (parotoid glands distinctly ovoid, about 1.5–2.0 times size of eyelid in *B. ibarrai*); and males usually with dorsal tubercles becoming spinose laterally and females with rounded tubercles middorsally (dorsal tubercles of males of *B. ibarrai* rounded laterally, and females with spinose middorsal tubercles). *Bufo coccifer* differs from *B. porteri* by having: sharply spinose lateral tubercles in males (rounded in males of *B. porteri*); and a relatively thin supratympanic crest (large, bulbous in *B. porteri*). Morphometric variation is summarized in Table 2.

Distribution and Ecology.—*Bufo coccifer* occurs along the Pacific versant of Mesoamerica, from the Guatemala-Mexico border to the Guanacaste region of Costa Rica (Fig. 6). Additional records exist from interior valleys on the Atlantic versant of Honduras and from the Atlantic coastal regions of Honduras and Nicaragua. McCranie and Wilson (2002) erroneously reported this species from the Atlantic versant of Guatemala; there are no records from this region. An apparently isolated population occurs in the southwestern region of the Isthmus of Tehuantepec, Oaxaca, Mexico. This species ranges from sea level to 1435 m (Savage, 2002; record from Cartago, Costa Rica) and occurs in a variety of tropical dry forests and savanna habitats. Duellman (1960) provided photographs of the habitat and some natural history observations from the Isthmus of Tehuantepec. McDiarmid and Foster (1981) described the reproductive biology of a population in northwestern Costa Rica. The ecological notes provided by McCranie and Wilson (2002) for Honduran populations represent mixed observations pertaining to *B. coccifer*, *B. ibarrai*, and *B. porteri*. Savage (2002) provided a concise summary of the ecology of this species, based on observations from Costa Rica.

Tadpole.—McDiarmid and Foster (1981) and Savage (2002) described tadpoles from Costa Rica and provided illustrations.

Table 2. Morphometric variation among males and females from of the *Bufo coccifer* complex; mean ± SD is presented above the range (in mm). Data for *B. ibarrai* taken, in part, from Mendelson (2001).

	B. coccifer	*B. cycladen*	*B. ibarrai*	*B. pisinnus*	*B. porteri*	*B. signifer*
Males	*n* = 130	*n* = 30	*n* = 79	*n* = 21	*n* = 43	*n* = 21
SVL	51.4 ± 4.8	51.1 ± 2.2	62.2 ± 9.1	45.9 ± 3.2	49.6 ± 4.6	51.2 ± 6.4
	41.0–64.4	47.4–54.2	42.5–82.4	38.5–51.4	40.2–58.7	42.0–64.1
Tibia length	18.3 ± 1.9	18.4 ± 0.9	24.1 ± 3.6	15.9 ± 1.4	18.4 ± 1.8	17.9 ± 2.3
	13.3–22.5	16.6–20.1	15.7–31.8	13.0–18.0	15.2–21.7	15.0–23.4
Foot length	18.1 ± 1.9	18.3 ± 0.7	24.6 ± 3.8	16.9 ± 1.3	18.8 ± 1.8	18.2 ± 2.3
	13.1–23.9	16.9–19.8	16.3–33.4	14.8–19.2	15.7–22.7	13.7–23.1
Head length	17.8 ± 1.8	18.0 ± 0.9	20.8 ± 2.8	15.1 ± 1.0	16.7 ± 1.4	17.4 ± 2.0
	13.6–21.6	16.7–20.9	15.3–26.5	12.9–17.1	14.0–20.0	14.7–22.2
Head width	20.5 ± 2.4	20.1 ± 0.9	23.9 ± 3.1	17.3 ± 1.4	18.9 ± 1.6	19.8 ± 2.4
	15.9–27.8	17.6–21.8	16.2–30.8	15.1–20.2	15.7–23.0	16.6–24.9
Tympanum	2.3 ± 0.5	2.7 ± 0.3	3.7 ± 0.7	2.3 ± 0.3	3.0 ± 0.4	3.1 ± 0.4
	1.3–3.7	2.1–3.3	2.7–5.3	1.8–2.6	2.2–3.5	2.5–3.8
Supratympanic crest	3.2 ± 0.5	2.7 ± 0.3	3.5 ± 0.5	2.6 ± 0.3	3.1 ± 0.3	3.0 ± 0.4
	2.0–4.4	2.2–3.3	2.3–5.2	2.2–3.2	2.3–3.7	2.1–3.8
Parotoid length	6.3 ± 1.0	6.9 ± 0.5	7.8 ± 1.5	5.4 ± 0.6	6.3 ± 0.9	6.3 ± 1.2
	4.3–8.7	6.0–4.8	3.2–11.0	4.1–6.5	5.0–9.0	2.8–8.8
Parotoid width	6.6 ± 1.3	6.1 ± 0.6	5.7 ± 0.9	5.3 ± 0.5	5.1 ± 0.7	6.0 ± 0.8
	3.7–9.5	5.0–7.2	3.5–7.4	4.5–6.2	3.8–6.7	4.6–7.7
Females	*n* = 25	*n* = 6	*n* = 61	*n* = 5	*n* = 14	*n* = 11
SVL	67.7 ± 7.6	59.8 ± 2.8	78.4 ± 7.6	59.1 ± 3.3	64.5 ± 5.8	67.2 ± 8.3
	58.1–82.4	54.6–62.9	60.8–94.4	55.4–62.2	56.4–73.0	54.5–77.0
Tibia length	22.2 ± 2.4	20.0 ± 1.6	28.7 ± 3.0	18.7 ± 1.1	22.5 ± 2.2	23.0 ± 3.4
	18.8–28.1	18.3–22.3	20.2–32.8	18.0–20.6	18.7–27.2	17.7–26.5
Foot length	21.9 ± 2.2	20.4 ± 1.0	28.7 ± 3.7	20.3 ± 1.3	22.5 ± 1.9	23.1 ± 3.7
	17.9–27.2	19.4–22.1	19.6–34.1	18.8–21.7	19.6–26.5	17.0–26.8
Head length	22.2 ± 2.2	20.7 ± 1.6	25.2 ± 2.1	18.8 ± 0.9	20.9 ± 2.0	22.6 ± 2.5
	19.2–26.8	18.9–22.8	19.8–28.5	17.6–19.7	18.0–25.9	18.4–25.9
Head length	25.5 ± 2.5	23.0 ± 1.5	29.5 ± 2.8	21.9 ± 1.2	23.9 ± 1.9	26.1 ± 3.4
	22.5–31.5	21.1–24.4	21.5–33.3	20.6–23.7	21.5–28.3	20.9–29.4
Tympanum	3.1 ± 0.6	2.8 ± 0.5	4.1 ± 0.5	3.2 ± 0.1	3.5 ± 0.5	3.6 ± 0.4
	2.1–4.2	2.2–3.5	3.0–5.4	3.1–3.4	2.6–4.5	3.1–4.3
Supratympanic crest	4.3 ± 0.8	3.1 ± 0.2	4.5 ± 0.7	3.4 ± 0.3	3.9 ± 0.6	4.0 ± 0.7
	2.9–6.2	2.8–3.4	2.9–6.0	3.1–3.8	3.0–5.2	3.1–5.2
Parotoid length	7.4 ± 1.3	7.6 ± 0.8	8.4 ± 1.5	6.8 ± 1.0	8.3 ± 08	7.8 ± 1.3
	5.4–9.9	6.5–8.5	3.0–11.7	5.9–8.4	6.8–9.9	5.5–9.9
Parotoid width	7.4 ± 1.1	6.9 ± 0.8	6.3 ± 0.9	6.6 ± 1.0	6.6 ± 0.4	7.7 ± 1.0
	5.7–10.4	6.2–8.4	4.1–8.2	5.6–7.8	6.1–7.2	5.4–9.0

Remarks.—Color photographs of this species appear in Leenders (2001:pl. 7), Savage (2002:pl. 77), and Villa (1972:fig. 57). Blair's (1963) reference to *Bufo coccifer* in his discussion of the evolution of North American bufonids is unclear because he does not give the provenance of the toads he analyzed. Lynch and Smith (1966) referred specimens from the Tehuantepec region of Oaxaca, Mexico to *B. cycladen*; however, this designation was not followed by most subsequent authors (Porter, 1967). Toads from the Tehuantepec region are distinct and allopatric, with respect to the toads we refer to *B. cycladen* on the slopes of the Sierra Madre del Sur in Guerrero and western Oaxaca.

There are no records of *Bufo coccifer* from the Pacific Coastal Plain of Chiapas, Mexico. Despite the lack of records in this region, we note that much of the region seems to be suitable subhumid habitat. Subhumid forest and scrub habitats extend along the coastal plain here, but grade into more humid forests along the base of Volcán Tacana (Johnson, 1989; Rzedowski, 1994). Although the lone specimen from Tapachula appears to have been found in a humid region, we note that the historical humid forests (W. E. Duellman, pers. comm.) along the coastal margin of Volcán Tacaná have been completely converted to crop and pasture lands (pers. obs.). Further fieldwork along the Pacific Coastal Plain of Chiapas is warranted to verify the allopatry of the population of *B. coccifer* in the Isthmus of Tehuanatepec, with respect to conspecifics in Guatemala. Johnson (1989) implied that *B. coccifer* occurs along the Pacific Coastal Plain of Chiapas, perhaps based on records from Soconusco, Chiapas, that were

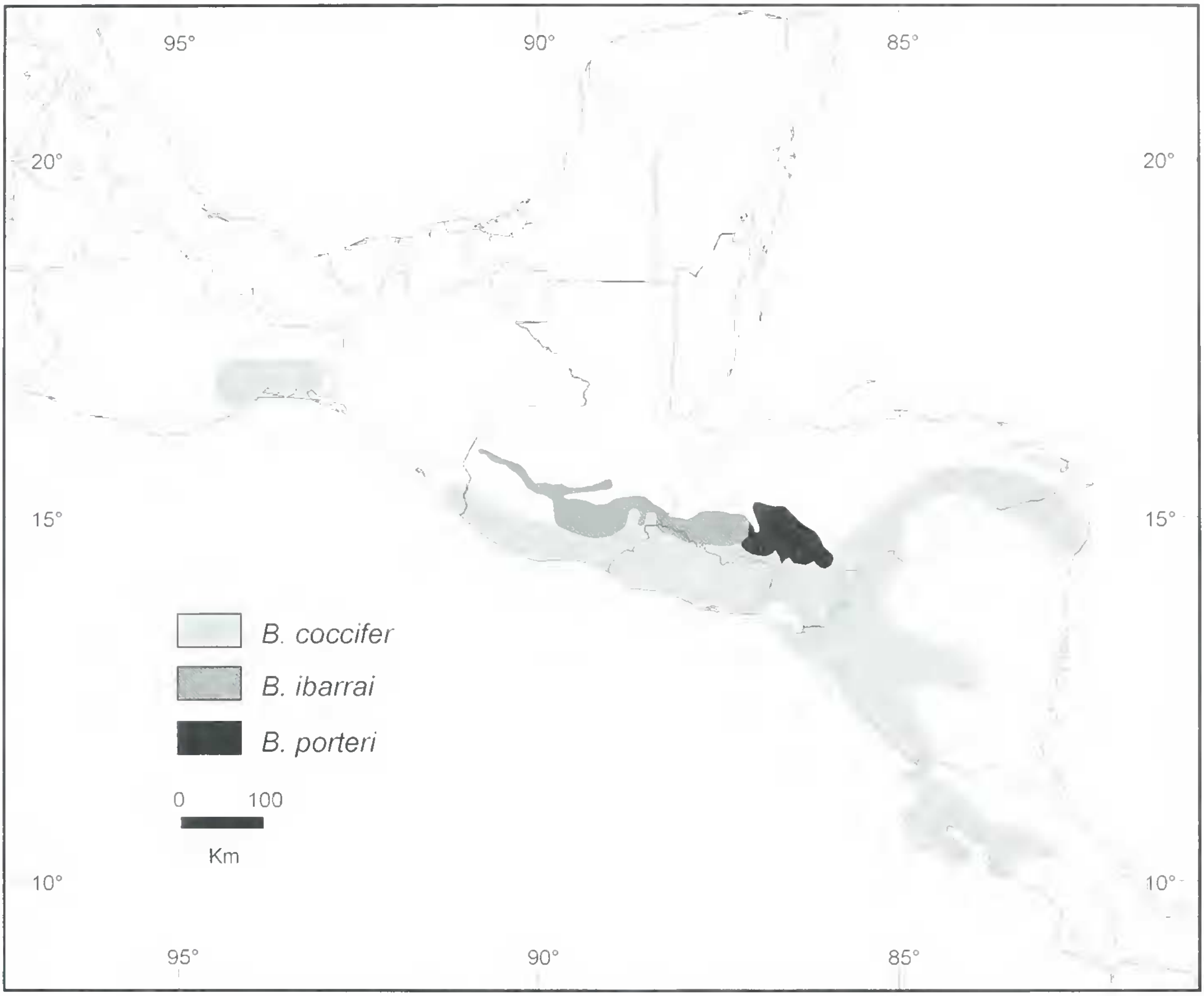

Fig. 6. Map of Central America showing the geographic distribution of *Bufo coccifer*, *B. ibarrai* and *B. porteri*.

listed by Porter (1963); these records actually represent misidentified specimens referable to *B. valliceps*. The single specimen from Tapachula, Chiapas (MVZ 177594), is a recently metamorphosed specimen that originally was misidentified as *B. luetkeni*. This record seems to be the source of information that resulted in *B. luetkeni* being listed incorrectly as part of the Mexican herpetofauna (Johnson, 1989; Flores-Villela, 1993)—*B. luetkeni* does not occur in Mexico. Johnson (1990) correctly stated that records of *B. coccifer* from the Grijalva Valley of Chiapas, Mexico, were based on misidentified specimens.

Bufo cycladen Lynch and Smith

Figs. 3–5

Bufo cycladen Lynch and Smith, 1966:19 Holotype: UIMNH 57142. Type locality: 3 mi [4.8 km] S Putla de Guerrero, Oaxaca, Mexico.

Bufo cycladen—Porter, 1967 [declared *nomen dubium*]; Frost, 1985 [in part]; Frost, 2003 [in part].

Bufo coccifer—Smith and Taylor, 1948 [in part]; Porter, 1963, 1965 [in part]; Villa et al., 1988 [in part]; Flores-Villela, 1993 [in part]; Campbell, 1999 [in part].

Diagnosis.— A small species of *Bufo* (males to 54 mm SVL; females to 62 mm SVL), having the following combination of characters: (1) tympanum evident externally, about 40–50% diameter of orbit in males, about 40–45% in females; (2) canthal, supraorbital, supratympanic, postorbital, preorbital, pretympanic, and supralabial crests present; (3) cranial crests well developed, robust, except parietal crest thin, low, or absent; (4) tibia short, about 34% SVL; (5) feet short, about 34 % SVL; (6) dorsal tubercles medium to large-sized, elevated, rounded, densely arranged on middorsal region, becoming large and conspicuously spinose laterally; (7) ventral tubercles relatively large, granular, with conspicuous spinose apices; (8) lateral descending row of enlarged tubercles absent; (9) skin texture not sexually dimorphic; (10) vocal slit unilateral in male; (11) *m. interhyoideus* poorly differentiated from *m. intermandibularis*, but differentiated posteriorly forming a large, unilobed vocal sac with heavy black pigmentation; (12) snout shape rounded in lateral view, pointed in dorsal view; (13) parotoid glands round to ovoid and large, about 1.5–2 times size of eyelid; (14) skin between cranial crests on top of head with few to many scattered, low, rounded tubercles; (15) ventral coloration whitish cream, with scattered dark brown, indistinct to distinct, punctuations in some individuals.

Bufo cycladen may be distinguished from all other members of the *Bufo coccifer* Group by the combination of: its relatively small size; relatively large, scattered, rounded tubercles on the middorsum; large, spinose tubercles on the dorsolateral and lateral surfaces; relatively large, spinose tubercles on the venter; large parotoid glands; weakly developed (or absent) parietal crest; and presence of scattered, dark brown punctations on the venter (but this last character is variable among specimens).

Bufo cycladen differs from *B. coccifer* by being smaller (males of *B. coccifer* to 62 mm SVL, females to 82 mm), and possessing the following characters: large, elevated, densely arranged middorsal tubercles (middorsal tubercles relatively small, scattered in *B. coccifer*); large, strongly spinose dorsolateral and lateral tubercles (dorsolateral and lateral tubercles smaller in *B. coccifer*, variably rounded or moderately spinose); relatively large, strongly spinose ventral tubercles (ventral tubercles small, rounded, or with tiny spinose apices in *B. coccifer*); weakly developed, or no, parietal crests (parietal crest relatively well developed in most specimens of *B. coccifer*); and an advertisement call with a higher pulse rate (Table 1, Fig. 2). *Bufo cycladen* differs from *B. pisinnus* by having: much larger, distinctly spinose dorsolateral tubercles (smaller, more rounded in *B. pisinnus*) and relatively larger parotoid glands (1–1.5 times size of eyelid in *B. pisinnus*). Superficially, *B. cycladen* resembles *B. signifer*, but it is smaller (males of *B. signifer* to 64 mm SVL, females to 77 mm) and has the following features: a whitish-cream venter, with or without scattered dark brown punctations (venter with bold brown-black marbling in *B. signifer*); and smaller and less spinose tubercles overall (but this latter character is somewhat variable and subjective). *Bufo cycladen* differs from *B. ibarrai* by: being smaller (males of *B. ibarrai* to 82 mm SVL, females to 94 mm); having males with conspicuously spinose dorsolateral and lateral tubercles; having relatively larger, more densely arranged middorsal tubercles (all such tubercles relatively small, scattered, rounded in males of *B. ibarrai*); and having rounded middorsal tubercles in females (tubercles spinose in females of *B. ibarrai*). *Bufo cycladen* differs from *B. porteri* by: having sharply spinose lateral tubercles in males (rounded in males of *B. porteri*); and relatively thin supratympanic crests (large, bulbous in *B. porteri*). Morphometric variation is summarized in Table 2.

Distribution and Ecology.—*Bufo cycladen* occurs in a relatively narrow elevational band along the Pacific slope of the Sierra Madre del Sur in Guerrero and Oaxaca, Mexico (Fig. 7). Most specimens have been collected at, or near, Agua del Obispo, Guerrero. Although commonly cited in the literature, Agua del Obispo does not appear on most maps because it is a private hacienda; it is located near the 1000-m contour (17°18′ N, 99°28′ W) along the old highway between the towns of Tierra Colorada and Chilpancingo, Guerrero. One other series (including the holotype, UIMNH 57142) is known from Putla de Guerrero, Oaxaca; this locality lies at an elevation similar to that of Agua del Obispo, Guerrero, about 150 km (airline) eastward on the same slope of the Sierra Madre del Sur.

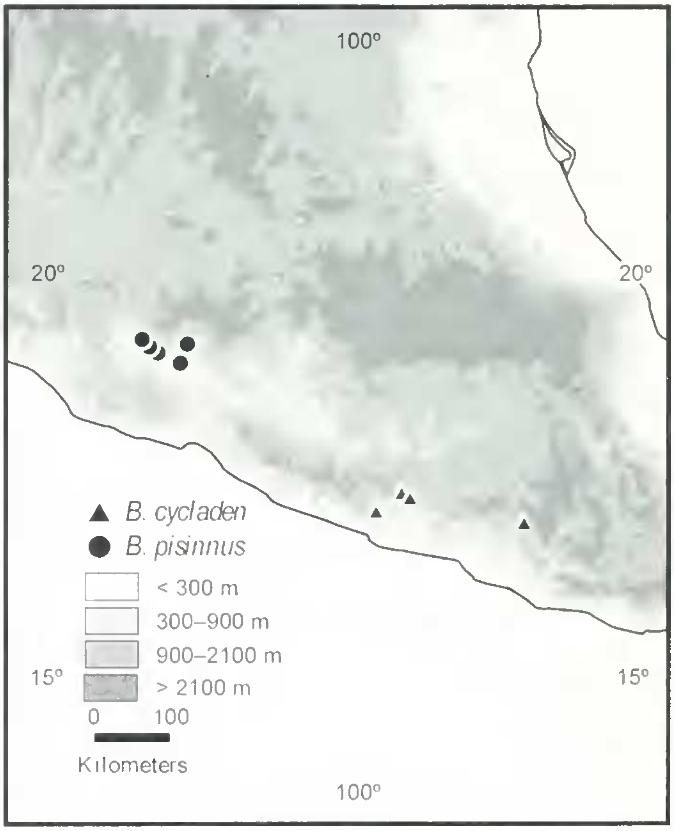

Fig. 7. Map of central Mexico with dot localities for *Bufo cycladen* and *B. pisinnus* (see species account below) indicating specimens examined, which represents all known localities.

Presumably, the distribution of this species is continuous along the middle-elevations of this slope, between these two localities. Campbell and Duellman (2000:19) described the habitat at Agua del Obispo as "…an area of scattered, small pines and brush that appears to be ecotonal between tropical deciduous forest, which is found slightly below, and pine-oak forest, which is present in the mountains above." Field work in this region by JRM and associates in 2000 and 2002 reinforced that *B. cycladen* seems to be restricted to this narrow, ecotonal habitat. In this area, we encountered: *B. marinus* and *B. marmoreus* at the lowest elevations between Acapulco and near Las Cruces; only *B. marmoreus* in the vicinity of Tierra Colorada (±900 m); *B. marinus* and *B. cycladen* near Agua del Obispo; only *B. perplexus* in the Zumpango del Río/Chichihualco area; and only *B. occidentalis* at high elevations (over 2000 m) near Carrizal de Bravo. Davis and Dixon (1965) reported some additional records of *Bufo* from along this transect, but we have not verified the identifications of those specimens. The sporadic appearance of *B. marinus* along this transect is noteworthy; we also note that Davis and Dixon (1965) did not report this species from anywhere in the area.

Tadpole.—The tadpole of *B. cycladen* is unknown, as are aspects of its reproductive biology. Davis and Dixon (1965) reported females collected on 22 June "…contained numerous small eggs."

Remarks.—The type locality for this taxon is near Putla, Oaxaca, Mexico, which is located at about 750 m elevation on the Pacific slope of the Sierra Madre del Sur; specimens designated as paratypes were collected at the type locality and from around Agua del Obispo, Guerrero, Mexico (Lynch and Smith, 1966). However, these authors referred all Mexican populations of *B. coccifer* to this new taxon (thereby including populations of three different species of toads, which we have identified as *B. coccifer*, *B. cycladen*, and *B. pisinnus*). Furthermore, it is evident from their map (Lynch and Smith, 1966:fig. 2) that their comparative samples of "*B. coccifer*" from Guatemala, Honduras, and Nicaragua may have included specimens that we recognize as *B. coccifer*, *B. ibarrai*, and *B. porteri*. Owing to this confusion, the diagnosis of *B. cycladen* presented in the original description has not been widely accepted (Porter, 1967; McDiarmid and Foster, 1981; Frost, 1985, 2003). We apply the taxon *B. cycladen* only to those populations on the Pacific slope of the Sierra Madre del Sur of Guerrero and Oaxaca, Mexico. It seems likely that the confusion associated with *B. cycladen* is the result of authors' having inadvertently compared a variety of different species in their efforts to distinguish *B. coccifer* and *B. cycladen*. Mendelson (2001) provided additional comments on this problem.

Bufo ibarrai Stuart

Figs. 3, 8, 9

Bufo ibarrai Stuart:159. Holotype: UMMZ 108000. Type locality Aserradero San Lorenzo [about 12 airline km slightly East of North of Jalapa], Jalapa, Guatemala, 1725 m.

Bufo coccifer—Cope, 1887 [in part]; Meyer and Wilson, 1971 [in part]; Campbell and Vannini, 1989 [in part]; Campbell, 1999 [in part]; McCranie and Wilson, 2002 [in part].

Bufo ibarrai—Lynch and Fugler, 1965 [in part]; Porter, 1966; Frost, 1985; Campbell, 1999; Mendelson, 2001; Frost, 2003.

Bufo microtis—Schmidt and Stuart, 1941 [in part, for reference to UMMZ 84083].

Diagnosis.—A large species of *Bufo* (males to 82.4 mm SVL; females to 94.4 mm SVL), having the following combination of characters: (1) tympanum evident externally, about 45% diameter of orbit in males, about 40% in females; (2) canthal, supraorbital, supratympanic, postorbital, preorbital, pretympanic,

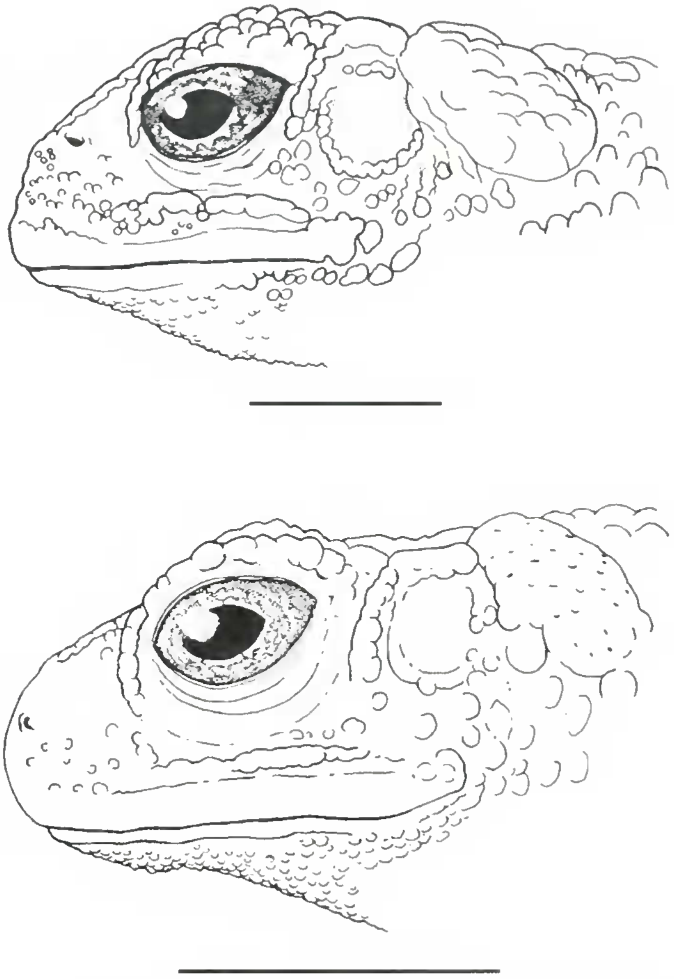

Fig. 8. Lateral aspects of the heads of adult male specimens of *Bufo ibarrai* (upper: KU 58413) and *B. pisinnus* (lower: UMMZ WED 233723; holotype). Scale bar = 1 cm.

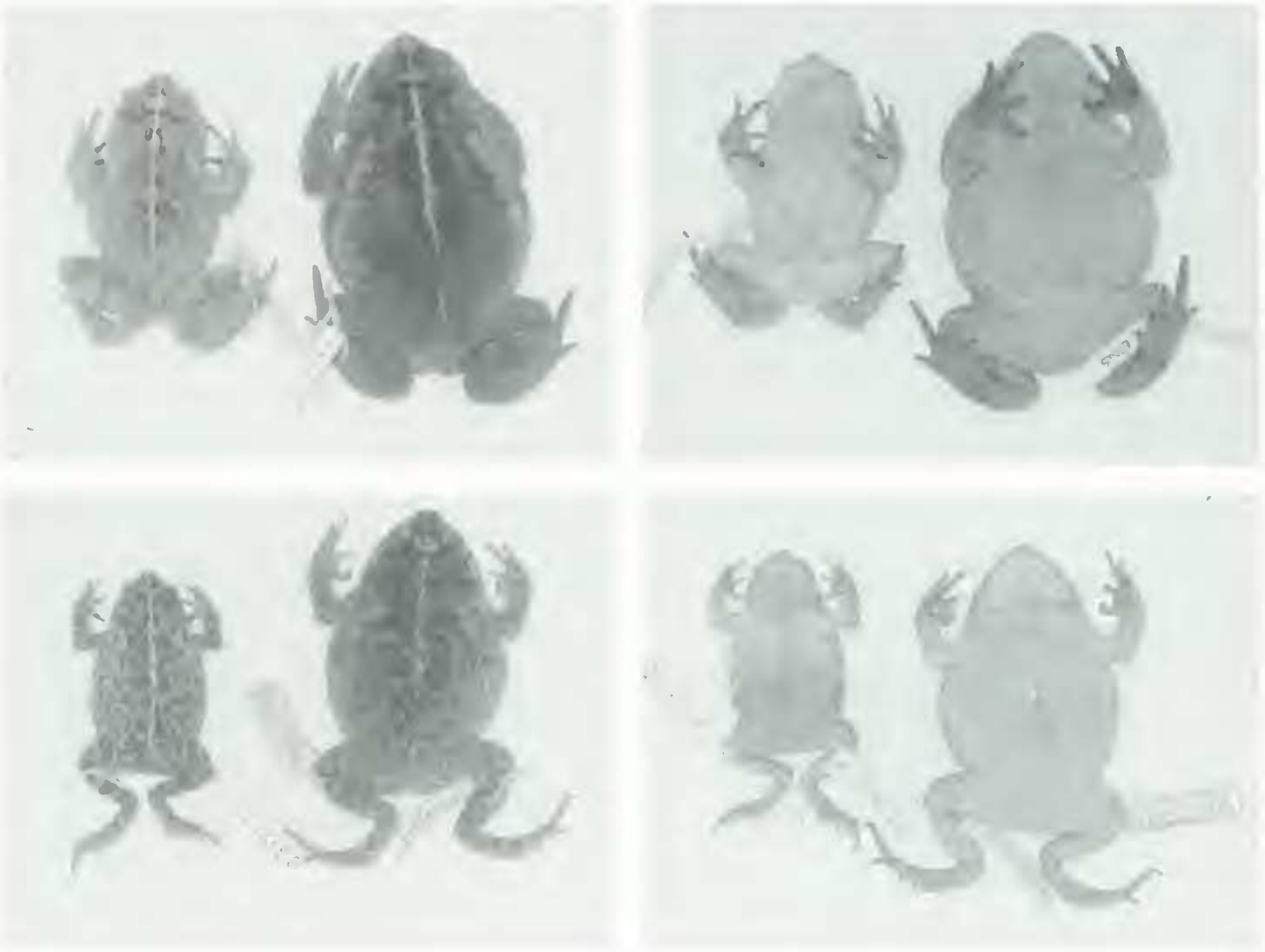

Fig. 9. Dorsal and ventral aspects of representative adult specimens of *Bufo ibarrai* from Departamento Guatemala, Guatemala (male, left: UTA A-25825, SVL = 69.8 mm; female, right: UTA A-47572, SVL = 93.3 mm) and *B. pisinnus* from Michoacán, Mexico (male, left: UMMZ 115353 [WED 10971], SVL = 43.5 mm; female, right. UMMZ 121578, SVL = 60.4 mm).

parietal, and supralabial crests present; (3) cranial crests well developed, parietal crests low, thin, sharply angled medially; supratympanic crest large, bulbous; (4) tibia short, about 40% SVL; (5) feet short, about 40% SVL; (6) middorsal tubercles sparse, rounded, becoming spinose laterally in females, all dorsal tubercles in males rounded, usually indistinct or absent laterally; (7) ventral tubercles areolate, non-spinose in males and finely spinose in females; (8) lateral descending row of enlarged tubercles indistinct or absent; (9) skin texture sexually dimorphic; (10) vocal slit unilateral in male; (11) *m. interhyoideus* poorly differentiated from *m. intermandibularis*, but differentiated posteriorly, forming a large, unilobed vocal sac with variable amounts of pigmentation; (12) snout shape rounded in lateral view, weakly pointed in dorsal view; (13) parotoid glands large, ovoid, length about 2 times size of eyelid; (14) skin between cranial crests usually smooth, lacking tubercles; (15) ventral coloration dull cream with some diffuse gray mottling in some individuals.

Bufo ibarrai is the largest species in the *B. coccifer* Group and differs from all species except *B. porteri* by: having relatively massive cranial crests, with the supratympanic crest being distinctly bulbous; and having sexually dimorphic skin texture with distinctly rounded lateral tubercles in males and spinose lateral tubercles in females. *Bufo ibarrai* closely resembles *B. porteri* but differs by: being larger (males to 82.4 mm SVL and females to 94.4 mm SVL vs. 59.9 mm in males and 76.2 mm in females); and having the caudal musculature of the tadpole uniform pale brown (cream and heavily punctated with brown in *B. porteri*). Morphometric variation is summarized in Table 2.

Distribution and ecology.—*Bufo ibarrai* occurs at moderate elevations (1360–1980 m) in the highlands of

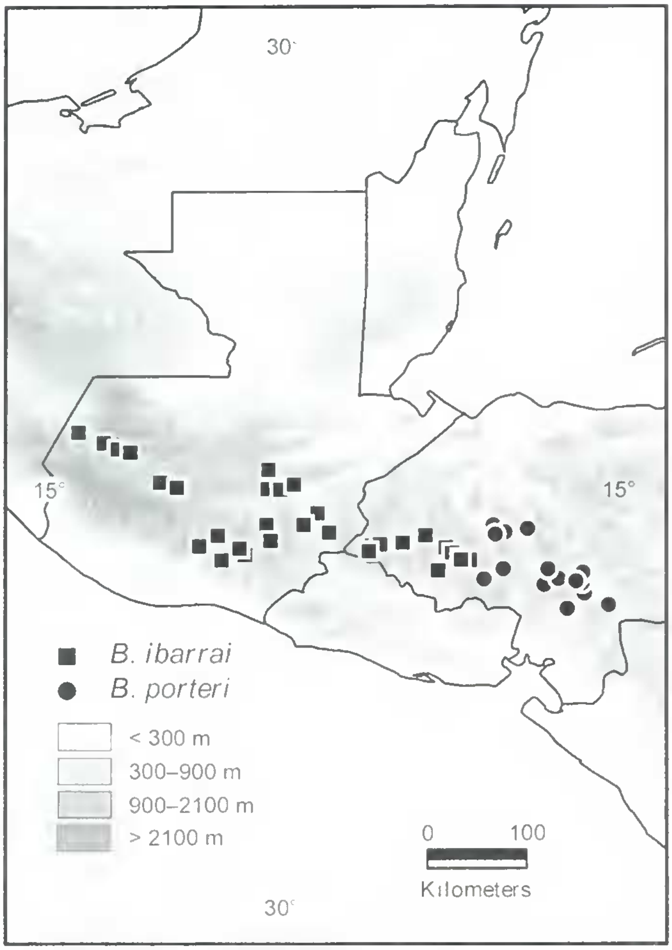

Fig. 10. Map of Guatemala and western Honduras with dot localities for *Bufo ibarrai* and *B. porteri* (see species account below) indicating specimens examined

central and southern Guatemala (Mendelson, 2001), and new information presented here extends that range into contiguous regions of Honduras (Fig. 10). The Honduran localities range up to 2020m elevation, and all represent Premontane Moist Forest (e.g., McCranie and Wilson, 2001: pl.2E) or Lower Montane Moist Forest (e.g., McCranie and Wilson, 2001:pl.4E) and lie in the western ranges of the Southern Cordillera Region (sensu McCranie and Wilson, 2001), in the departments of Intibuca, Lempira, and Ocotepeque (Fig. 10). These discoveries refute Mendelson's (2001) premature speculation that *B. ibarrai* may be endemic to Guatemala and refute McCranie and Wilson's (2001) conclusion that *B. ibarrai* does not occur in Honduras.

Tadpoles.—The tadpole was described by Mendelson (2001).

Remarks.—Although Mendelson (2001) discussed diagnostic features that distinguish *B. coccifer* and *B. ibarrai*, he did not present multivariate analyses of morphometry. In addition, Mendelson's (2001) research was based only on specimens from Guatemala. During the course of this study, Eric N. Smith kindly sent to us specimens of *B. ibarrai* he collected in Ocotepeque, Honduras. These toads are consistent with the diagnosis presented by Mendelson (2001) and have a similar (0.67% divergent) mitochondrial-DNA sequence to *B. ibarrai* collected at the opposite end of the range of the species, in El Quiche, Guatemala. We also discovered additional specimens from western Honduras among museum collections (Appendix II) that match the diagnosis provided by Mendelson (2001); these specimens

Bufo ***pisinnus*** new species

Figs. 3, 8, 9

Bufo coccifer Porter, 1963 [in part]; Frost, 1985 [in part]; Villa et al., 1988 [in part]; Flores-Villela, 1993 [in part]; Campbell, 1999 [in part]; Frost, 2003 [in part].

Bufo cycladen Lynch and Smith, 1966 [in part, for reference to specimens from Michoacan, Mexico].

Holotype.—UMMZ 233723 (WED 10973), an adult male from 6.2 mi [10 km] E Apatzingán, 1100 feet [335 m] elevation, obtained by W. E. Duellman and R. E. Etheridge on 2 August 1956.

Paratypes.—All from Michoacán, Mexico: 6.2 mi [10 km] E Apatzingán, 1100 ft [335 m] (UMMZ 115353 [15 specimens]); 7 mi [11.2 km] E Apatzingán, 1100 ft [335 m] (UMMZ 112794 [6 specimens), 115355); 1 mi [1.6 km] W Apatzingán, 1100 ft [335 m] (UMMZ 115354); 3 mi [4.8 km] S Lombardia (UMMZ 121578).

Diagnosis.—A small species of *Bufo* (males to 51 mm SVL; females to 62 mm SVL), having the following combination of characters: (1) tympanum evident, about 35–40% diameter of orbit in males, about 40–50% in females; (2) canthal, supraorbital, supratympanic, postorbital, preorbital, pretympanic, supralabial crests present, parietal crest a thin ridge, or absent; (3) cranial crests weakly developed, thin, low; (4) tibia short, about 34% SVL; (5) feet short, about 36% SVL; (6) dorsal tubercles small to medium sized, low, rounded, relatively densely arranged middorsally, becoming smaller and spinose laterally; (7) ventral tubercles tiny, evenly granular, appearing smooth, especially in males, but tiny, spinose apices apparent under microscope; (8) lateral descending row of enlarged tubercles absent; (9) skin texture not sexually dimorphic; (10) vocal slit unilateral in male; (11) *m. interhyoideus* poorly differentiated from *m. intermandibularis*, but differentiated posteriorly forming a large, unilobed vocal sac with heavy black pigmentation; (12) snout shape acutely rounded in lateral view, sharply pointed in dorsal view, snout shape in females similar but more gently rounded in lateral view; (13) parotoid glands ovoid, about 1.0–1.5 times size of eyelid; (14) skin between cranial crests on top of head usually with many scattered, low, rounded tubercles; (15) ventral coloration usually immaculate whitish cream, some individuals with tiny, scattered black flecks.

Bufo pisinnus can be distinguished from all other members of the *B. coccifer* Group by its small size, and possession of: relatively weakly developed cranial crests, the parietal crest appearing only as a thin ridge among surrounding tubercles and frequently is absent; smaller, more densely arranged dorsal tubercles; and smaller, less spinose ventral tubercles. *Bufo pisinnus* differs from *B. coccifer* by having: a relatively shorter snout and an advertisement call with a higher pulse rate (120 pulses per sec vs. maximum of 115 pulses; Table 1, Fig. 2). *Bufo pisinnus* differs from *B. cycladen* by having: much smaller, and less spinose dorsolateral tubercles (large and conspicuously spinose in *B. cycladen*); and smaller parotoid glands (about 1.5–2.0 times size of eyelid in *B. cycladen*). *Bufo pisinnus* differs from *B. signifer* by having: a whitish-cream venter, with or without scattered black flecks (venter with bold brown-black marbling in *B. signifer*); smaller parotoid glands (about twice size of eyelid in *B. signifer*); and an advertisement call with a higher frequency and faster pulse rate (Table 1, Fig. 2). *Bufo pisinnus* differs from *B. ibarrai* by having: smaller, more rounded parotoid glands (glands in *B. ibarrai* ovoid, much higher, and about twice size of the eyelid); and rounded mid-dorsal tubercles in both sexes (tubercles in *B. ibarrai* rounded in males, spinose in females). *Bufo pisinnus* differs from *B. porteri* by having: sharply spinose lateral tubercles in males (rounded in males of *B. porteri*); and a relatively thin supratympanic crest (large, bulbous in *B. porteri*).

Description of holotype.—Body robust; head wider than long, width 39.1% SVL, length 35.3% SVL; snout sharply pointed in dorsal view, rounded in profile, rostral keel distinct; canthal, preorbital, supraorbital, pretympanic, supratympanic, and postorbital crests present, distinct; parietal crests reduced, barely distinct; skin on top of head co-ossified; nostril not protuberant, directed dorsally; canthus rostralis forming distinct, raised, canthal crest; loreal region concave; lip distinct, rounded; suborbital crest present, distinct, extending from angle of the jaw anteriorly to level of anterior margin of orbit; notch at symphysis of upper jaw present, distinct; eye–nostril distance 5.7% diameter of orbit; tympanum distinct, nearly round; tympanic annulus distinct only along anterior and ventral margins, upper margin contacting supratympanic crest, posterior margin obscured by overlying flesh. Forelimb short, robust; hand broad, with short, slender fingers; relative length of fingers: II < I < IV < III, webbing and lateral fringe on fingers absent; tips of fingers not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; palmar tubercle distinct, large, ovoid; pollical tubercle smaller than palmar tubercle, ovoid; subarticular tubercles distinct, elevated, triangular in profile, single except distal tubercle on Finger III bifid; supernumerary tubercles of unequal size, small, distinct, scattered evenly over palm and ventral surfaces of fingers; nuptial excrescences present as brown granular patches on medial surfaces of Fingers I and II. Hind limbs short, slender, tibia length 35.8% SVL; foot length 38.0% SVL; tarsal fold absent; outer metatarsal tubercle minute, elevated, ovoid; inner metatarsal tubercle slightly larger than outer metatarsal tubercle, distinctly elevated, ovoid; toes long, slender, relative lengths of toes: I < II < V < III < IV; lateral fringe present on Toes II, III, and V, absent on Toes I and IV; webbing thin, webbing formula I1—3II2—3III2—4IV4—2V; tips of toes not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; subarticular tubercles distinct, elevated, triangular in profile, bifid; supernumerary tubercles unequal in size, distinct, distributed evenly over ventral surfaces of foot and toes.

Skin on dorsum of body rugose with evenly distributed, small, rounded tubercles of relatively equal size, becoming sharply pointed laterally; parotoid glands about same size as eyelids, ovoid, oriented perpendicular to midline of body; lateral row of enlarged tubercles barely evident; dorsal surface of head smooth with few, small, rounded tubercles scattered in interspaces between cranial crests; dorsal surfaces of limbs covered with small, weakly pointed tubercles; skin on throat and other ventral surfaces granular, covered with tiny flattened and weakly pointed tubercles.

Choanae small, rounded, widely spaced; teeth and odontoids absent; tongue long, ovoid, about four times as long as wide, free posteriorly for about one-fourth its length; vocal slit unilateral, sinistral.

Coloration of holotype.—In preservative (ethanol), dorsum of body and limbs mottled evenly with pale brown and dark brown markings; irregular cream blotches present posterior to each parotoid gland; top of head uniform dark brown with distinct cream interorbital bar; distinct cream middorsal stripe extending from snout to posterior end of urostyle, irregularly widened at several points along its length; lateral surfaces pale brown with dark brown flecking. Ventral surfaces nearly immaculate cream; dark vocal sac visible through gular skin.

Measurements of the holotype (in mm).— SVL 45.0, HL 15.9, HW 17.6, TL 16.1, FL 17.1, orbit diameter 5.4, tympanum diameter 2.5, supratympanic crest length 2.7, parotoid gland length 5.4, parotoid gland width 4.8.

Coloration in life.—Duellman (1961:21) described coloration "...yellowish tan ground color with dark brown spots; middorsal stripe is deep yellow or cream color. The venter is dusty cream color, and the iris is pale gold."

Variation.—Morphometric variation among specimens examined is summarized in Table 2. The parietal crest is poorly developed in most specimens, and essentially absent in a few individuals (e.g., UMMZ 121578). Some individuals (e.g., UMMZ 112794) have a dark-brown ground color on the dorsum, which effectively obscures the dark brown dorsal blotches; most specimens have a pale brown to grayish ground color on the dorsum, and the overlying brown blotches are distinct. The brown blotches on the dorsum may be relatively small, incorporating one to three dorsal tubercles (e.g., UMMZ 115353 [WED 10972]), or the blotches may be larger, incorporating more than 12 dorsal tubercles (e.g., UMMZ 115353 [WED 10974]). The narrow middorsal cream stripe invariably is present in all individuals examined. Scattered black flecks on the ventral surface may be absent (*e.g.*, UMMZ 121578), restricted to the peripheral ventral surfaces (e.g., UMMZ 115353 [WED 10970]), or scattered relatively evenly across the venter (e.g., UMMZ 115354 [WED 10976]).

Etymology.—The name *pisinnus* is the Latin word *pisinnus*, meaning small, in reference to the diminutive size of this species.

Distribution and ecology.—*Bufo pisinnus* is known only from the Tepalcatepec Valley, which represents the western extension of the Balsas Basin (Fig. 7). Duellman (Field Notes, 16 July 1960) described the area around Lombardia, Michoacán, as having grassy areas interrupted by areas of mesquite with many reddish rocks and barren areas. Duellman (1961) suggested that this species is likely widespread in region, but noted that it does not occur along the coast of Michoacán. Duellman (1961) reported breeding choruses in muddy ditches and flooded grassy fields after heavy rains in June and August.

Tadpoles.—The tadpole of *B. pisinnus* is unknown.

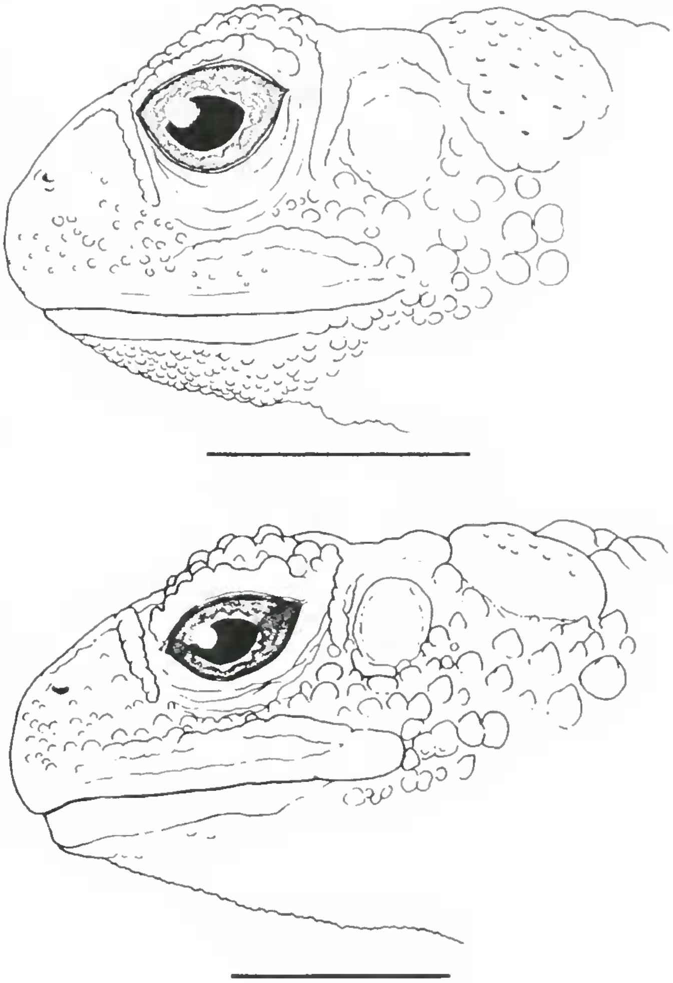

Fig. 11. Lateral aspects of the heads of adult male specimens of *Bufo porteri* (upper: KU 97520) and *B. signifer* (lower: AMNH 69626). Scale bar = 1 cm.

Bufo **porteri** new species

Figs. 3, 11, 12

Bufo coccifer—Meyer and Wilson, 1971 [in part]; Frost, 1985 [in part]; McCranie and Wilson, 2002 [in part]; Campbell, 1999 [in part]; Frost, 2003 [in part].

Bufo ibarrai—Lynch and Fugler, 1965 [in part].

Holotype.—KU 97519, and adult male from 6 mi [9.6 km] NE Escuela Panamericana, Cerro Uyuca, 5200 ft [1584 m], Francisco Morazán, Honduras, obtained by K. R. Porter on 30 June 1964.

Paratypes.—All from Franciso Morazán, Honduras: 6 mi [9.6 km] NE Escuela Panamericana, Cerro Uyuca, 5200 ft [1584 m] (KU 97520–26); 6 mi [9.6 km] NE Escuela Panamericana, Cerro Uyuca, 6000 ft [1828 m] (KU 97514); W slope Cerro Uyuca, 1650 m (KU 103221); Parque Nacional La Tigra above San Juancito, 2100 m (KU 192294); Cerro La Tigra, 1840–1890 m (KU 194216–19, 209249).

Diagnosis.—A small to medium-sized species of *Bufo* (males to 59.9 mm SVL; females to 76.2 mm SVL), having the following combination of characters: (1) tympanum evident externally, about 40% diameter of orbit in both males and females; (2) canthal, supraorbital, supratympanic, postorbital, preorbital, pretympanic, parietal, and supralabial crests present; (3) cranial crests well developed, parietal crests low, thin, supratympanic crest large, bulbous; (4) tibia short, about 37% SVL; 5) feet short, about 37% SVL; (6) middorsal tubercles sparsely arranged, rounded, becoming spinose laterally in females, all dorsal tubercles in males rounded, usually becoming indistinct or absent laterally; (7) ventral tubercles areolate, non-spinose in males, finely spinose in females; (8) lateral descending row of enlarged tubercles indistinct or absent; (9) skin texture sexually dimorphic; (10) vocal slit unilateral in male; (11) *m. interhyoideus* poorly differentiated from *m. intermandibularis* differentiated posteriorly, forming a

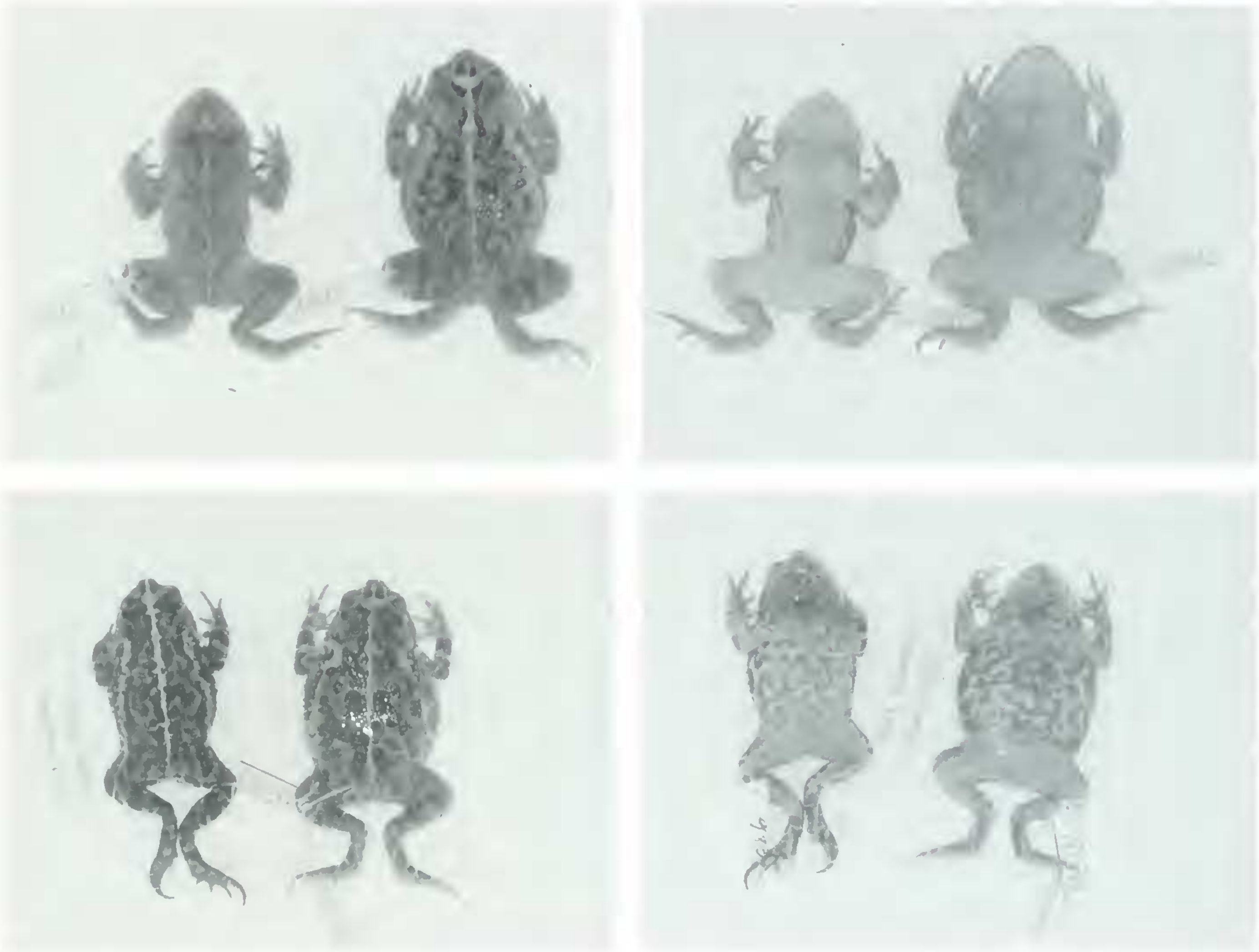

Fig. 12. Dorsal and ventral aspects of representative adult specimens of *Bufo porteri* from Francisco Morazán, Honduras (male, left: KU 97519, SVL = 51.6 mm; female, right: KU 97514, SVL = 60.7 mm) and *B. signifer* Panama (adult male, left: TNHC 31341, SVL = 49.7 mm, subadult female, right: KU 115359, SVL = 54.1 mm).

large, unilobed vocal sac heavily pigemented in black; (12) snout shape rounded in lateral view, weakly pointed in dorsal view; (13) parotoid glands moderate, round to ovoid, length about 1.00–1.25 times size of eyelid; (14) skin between cranial crests usually smooth, lacking tubercles; (15) ventral coloration is dull cream with some diffuse gray mottling in some individuals.

Bufo porteri may be distinguished from all other member of the *B. coccifer* Group, except *B. ibarrai*, the sexual dimorphism in the texture of the dorsal skin and the relatively robust cranial crests, especially the supratympanic crest. *Bufo porteri* closely resembles *B. ibarrai* but differs by being smaller (males to 59.9 mm SVL and females to 76.2 mm SVL vs. males to 82.4 mm SVL and females to 94.4 mm SVL); adult male *B. porteri* as small as 43.9 mm SVL have been observed (e.g., LSUMZ 46431). The caudal musculature of the tadpole of *B. porteri* is cream with heavy brown punctations (See description by McCranie and Wilson, 2002:173; caudal musculature in *B. ibarrai* is uniform pale brown.)

Description of holotype.—Body robust; head wider than long, width 40.0% SVL, length 36.4% SVL; snout sharply pointed in dorsal view, pointed in profile, rostral keel distinct; canthal, preorbital, supraorbital, pretympanic, supratympanic, and postorbital crests present, distinct; supraorbital and supratympanic crests distintly thickened; parietal crests present, not reduced; skin on top of head co-ossified; nostril protuberant, directed dorsally; canthus rostralis forming distinct, raised, canthal crest; loreal region concave; lip distinct, rounded; suborbital crest present, distinct, extending from angle of the jaw anteriorly to level of anterior margin of orbit; notch at symphysis of upper jaw present, distinct; eye–nostril distance 57.9% diameter of orbit; tympanum distinct, nearly round; tympanic annulus distinct only along anterior, ventral, and posteroventral margins; upper margin of tympanic annulus contacting and obscured by supratympanic crest. Forelimb short, robust; hand broad with short, slender fingers; relative length of fingers: II < I < IV < III, webbing and lateral fringe on fingers absent; tips of fingers not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; palmar tubercle distinct, large, rounded; pollical tubercle smaller than palmar tubercle, rounded; subarticular tubercles distinct, elevated, triangular in profile, all single except distal tubercle on Finger III bifid; supernumerary tubercles of unequal size, small, distinct, scattered evenly over palm and ventral surfaces of fingers; nuptial excrescences present as brown granular patches on medial surfaces of Fingers I–III. Hind limbs relatively long, slender, tibia length 41.7% SVL; foot length 40.5% SVL; tarsal fold absent; outer metatarsal tubercle very small, rounded, indistinct; inner metatarsal tubercle much larger than outer metatarsal tubercle, distinctly elevated, ovoid; toes long, slender, relative lengths of toes: I < II < V < III < IV; lateral fringe barely evident on Toes III and IV, absent on other toes; webbing thin, webbing formula **I**1 — 3**II**2 — 3**III**2 — 4**IV**4 — 2V; tips of toes not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; subarticular tubercles distinct, elevated, triangular in profile, bifid on Toes III and IV; supernumerary tubercles unequal in size, distinct, distributed evenly over ventral surfaces of foot and toes.

Skin on dorsum of body relatively smooth with scattered, small, rounded tubercles of unequal size, many bearing tiny, indistinct single keratinized apices; tubercles on lateral surfaces indistinct, rounded or ovoid, not pointed; parotoid glands about same size as eyelids, ovoid, oriented slightly divergent to midline of body; distinct lateral row of enlarged tubercles absent; dorsal surface of head smooth with few, small, rounded tubercles scattered in interspaces between cranial crests; dorsal surfaces of limbs covered with small weakly pointed tubercles; skin on throat and other ventral surfaces smoothly granular.

Choanae moderate in size, rounded, widely spaced; teeth and odontoids absent; tongue long, ovoid, about four times as long as wide, free posteriorly for about one-fourth its length; vocal slit unilateral, dextral.

Coloration of holotype.—In preservative (ethanol), body pale brown with indistinct, medium-brown marbled markings diffused across middorsal and lateral areas; distinct, thin cream middorsal stripe present; two oblong dull cream patches on dorsolateral areas; distinct dark brown bar extending across area between parietal crests and another covering area between canthal crests; all limbs with indistinct medium brown crossbars; venter immaculate dull cream; dark vocal sac clearly visible through gular skin.

Measurements of the holotype (in mm).— SVL 51.3, HL 18.7, HW 20.5, TL 21.4, FL 20.8, orbit diameter 7.6, tympanum diameter 3.0, supratympanic crest length 3.1, parotoid gland length 6.9, parotoid gland width 4.8.

Coloration in life.— McCranie and Wilson (2002:pl 9D) provided a color photograph of this speceis; see also Figure 3.

Variation.—Morphometric variation among specimens examined is summarized in Table 2. The parietal crests in females generally are well developed and distinct; however, the condition of the crest varies among males and may be relatively robust (e.g., KU 209249) or reduced to an indistinct, thin sliver of raised bone (e.g., KU 97523). The brown dorsal blotches may be very dark brown, and therefore quite distinct (e.g., LSUMZ 46398), or they may be only slightly darker than the brown ground color of the dorsum (e.g., LSUMZ 46445). The ventral coloration is either uniform dull cream (e.g., KU 103221) or bearing diffuse, grayish-brown marbling that ranges from moderate (e.g., KU 97522) to extensive (e.g., KU 194216). The middorsal cream stripe invariably is present on all individuals examined; this stripe is quite indistinct in a small number of individuals (e.g., KU 97520) and may appear irregular (i.e., not forming a straight line; e.g., LSUMZ 45441).

Etymology.—The specific epithet is a patronym that honors Kenneth R. Porter and his series of papers (e.g., Porter, 1963, 1964, 1965) on the systematics of Mesoamerican *Bufo*, and also recognizes his numerous field efforts that resulted in many of specimens referred to herein.

Distribution and ecology.—*Bufo porteri* is known from the Honduran departments of Comayagua, Francisco Morazán, and La Paz (Fig. 10). The known localities for this species generally represent Lower Montane Moist Forest habitats (e.g., McCranie and Wilson, 2001:pl. 4C) in the Montañas de Comayagua region. These localities differ markedly from the lower elevation, Dry and Arid Forest habitats (e.g., McCranie and Wilson, 2001:pl.1C) occupied by *B. coccifer*.

Tadpoles.—Tadpoles referrable to *B. porteri* (based on geography) were described by McCranie and Wilson (2002:173). The tadpole of this species resembles that of *B. coccifer* (McDiarmid and Foster, 1981; Savage, 2002), from which it is distinguished by having submarginal papillae on the oral disc (absent in *B. coccifer*) and cream-colored caudal musculature with brown punctations (boldly marked with brown saddles in *B. coccifer*).

Remarks.—We have allocated many Honduran specimens that previously were referred to *B. coccifer* (e.g., McCranie and Wilson, 2001) to the new taxon *B. porteri*, or to *B. ibarrai* (discussed above, and Appendix II). The difficulty of identifying specimens from this country is exacerbated by the resemblance of *B. porteri* and *B. ibarrai*. The wide range of variation among specimens of "*B. coccifer*" from Honduras described by McCranie and Wilson (2001) seems to be attributable to the fact that three relatively similar species occur in close proximity in that country.

At a general level, this species appears to be parapatric with respect to the distribution of *Bufo coccifer*. Thus, the distribution and habitat associations of this species, with respect to those of *B. coccifer*, resemble the relationship between *B. coccifer* and *B. ibarrai* in Guatemala as described by Mendelson (2001). Inasmuch as species of *Bufo* frequently are interfertile (Blair, 1963; Masta et al., 2002), it is possible that *B. porteri* may hybridize with *B. coccifer* if the species co-occur on the lower slopes of the Pacific Versant of Honduras. Similarly, hybrids between *B. porteri* and *B. ibarrai* eventually may be found.

Bufo ***signifer*** new species

Figs. 3, 11, 12

Bufo coccifer Dunn, 1933; Zweifel, 1965; Frost, 1985 [in part, for reference to specimens from Panama]; Villa et al., 1988 [in part, for reference to records from Panama]; Campbell, 1999 [in part].

Holotype.—AMNH 69626, an adult male from 7 mi N [11.2 km] and 2 mi [3.2 km] W of David, Chiriquí, Panama, obtained by R. G. Zweifel on 25 June 1962.

Paratypes.—All from Panama. Chiriquí: 7 mi [11.2 km] E Concepción (AMNH 69627); 2.5 mi [4.0 km] NE David (TNHC 3134–43); 23 km NNE San Felix, 900 m (USNM 297511–21). Cocle: El Valle de Anton (AMNH 59634, 59637); 16 km S, 9 km W Penonome, 30 m (KU 115359–61); 3.2 km W Agua Dulce, 15 m (KU 115362). Herrera: Jacinto, 2250 ft [686 m] (ANSP 22341–44); 3 mi [4.8 km] SW Pan American Hwy, on road past Potuga (UMMZ 167373). Veraguas: 14 km NE Sona, 75 m (KU 95432).

Diagnosis.— A medium-sized species of *Bufo* (males to 64 mm SVL; females to 77 mm SVL), having the following combination of characters: (1) tympanum evident externally, about 40–45% diameter of orbit in males, about 40–50% in females; (2) canthal, supraorbital, supratympanic, postorbital, preorbital, pretympanic, parietal and supralabial crests present; (3) most cranial crests distinct and thick, except parietal crests low, thin, sometimes intermittent; (4) tibia short, about 35% SVL; (5) feet short, about 36% SVL; (6) dorsal tubercles medium-sized, prominent, rounded, relatively densely arranged middorsally, becoming smaller, more concentrated, and spinose laterally; (7) ventral tubercles granular, with small, distinct spinose apices; (8) lateral descending row of enlarged tubercles absent; (9) skin texture not sexually dimorphic; (10) vocal slit unilateral in male; (11) *m. interhyoideus* poorly differentiated from *m. intermandibularis*, but differentiated posteriorly forming a large, unilobed vocal sac with heavy black pigmentation; (12) snout shape rounded in lateral view, pointed in dorsal view; (13) parotoid glands round to subovoid, about twice size of eyelid; (14) skin between cranial crests on top of head usually with few, scattered, low, rounded tubercles; (15) ventral coloration cream with distinct, bold, brown-black marbled pattern, becoming indistinct over pelvic patch.

Bufo signifer may be distinguished from all other members of the *Bufo coccifer* Group by having a cream venter overlain with a distinct, marbled pattern of brown-black markings. All other species in the group have immaculate, or nearly immaculate, cream ventral surfaces with the exception that some individuals of *B. cycladen* may have some dark brown mottling, and some individuals of *B. pisinnus* may have some tiny, black flecks. *Bufo signifer* differs from *B. coccifer* by having: relatively thinner and lower parietal crests (typically higher and thicker in *B. coccifer*); relatively smaller tympana; and an advertisement call with a lower frequency and pulse rate (Table 1, Fig. 2). *Bufo signifer* is superficially quite similar to *B. cycladen* but differs by: being larger (males of *B. cycladen* to 54 mm SVL, females to 62 mm); having a distinctly marbled ventral pattern (variably present, but always less developed in *B. cycladen*); and having generally smaller, less spinose tubercles overall (but this latter character is somewhat variable and subjective). *Bufo signifer* differs from *B. pisinnus* bybeing larger (males of *B. pisinnus* to 51 mm SVL, females to 62 mm) and by having: larger middorsal tubercles (small in *B. pisinnus*); larger parotoid glands (glands about 1.0–1.5 times size of eyelid in *B. pisinnus*); spinose tubercles on the venter (granular, non-spinose in *B. pisinnus*); an advertisement call with a lower frequency and pulse rate (Table1, Fig. 2); and better-developed cranial crests, especially with respect to the parietal crest (crests weakly developed, and parietal crest very reduced or absent in *B. pissinus*). *Bufo signifer* differs from *B. ibarrai* by being smaller (males of *B. ibarrai* to 82 mm SVL, females to 94 mm) and by having: smaller, more rounded parotoid glands (glands in *B. ibarrai* ovoid, about twice the size of the eyelid); and rounded mid-dorsal tubercles in both sexes (tubercles in *B. ibarrai* rounded in males, spinose in females). *Bufo signifer* differs from *B. porteri* by having: sharply spinose lateral tubercles in males (rounded in males of *B. porteri*); and a relatively thin supratympanic crest (large, bulbous in *B. porteri*).

Description of holotype.—Body robust; head wider than long, width 39.9% SVL, length 34.7% SVL; snout sharply pointed in dorsal view, rounded in profile, rostral keel distinct; canthal, preorbital, supraorbital, pretympanic, supratympanic, and postorbital crests present, distinct;

parietal crests present, relatively indistinct; skin on top of head coossified; nostril protuberant, directed dorsally; canthus rostralis forming distinct, raised, canthal crest; loreal region concave; lip distinct, rounded; suborbital crest present, distinct, extending from angle of the jaw anteriorly to level midway between orbit and nostril; notch at symphysis of upper jaw present, shallow, indistinct; eye–nostril distance 47.6% diameter of orbit; tympanum distinct, nearly round; tympanic annulus distinct only along anteroventral margin, upper margin contacting supratympanic crest, posterior margin obscured by overlying flesh. Forelimb short, robust; hand broad, with short, slender fingers; relative length of fingers: II < I < IV < III, webbing and lateral fringe on fingers absent; tips of fingers not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; palmar tubercle distinct, large, round; pollical tubercle smaller than palmar tubercle, ovoid; subarticular tubercles distinct, elevated, triangular in profile, single except distal tubercle on Finger III bifid; supernumerary tubercles of unequal size, large, distinct, scattered evenly over palm and ventral surfaces of fingers; nuptial excrescences present as brown granular areas on entire dorsal surfaces of Fingers I and II, including lateral surfaces of tips of fingers, lateral surfaces of distal phalange of Finger III, and on medial surface of pollical tubercle. Hind limbs short, slender, tibia length 34.5% SVL; foot length 35.1% SVL; tarsal fold absent; outer metatarsal tubercle small, elevated, ovoid; inner metatarsal tubercle slightly larger than outer metatarsal tubercle, distinctly elevated, ovoid; toes long, slender, relative lengths of toes: I < II < V < III < IV; lateral fringe on toes barely evident on Toes II and III, absent on other toes; webbing thin, webbing formula I1 — $2^{1}/_{4}$II$1^{1}/_{4}$ — 3III2 — 4IV4 — 2V; tips of toes not enlarged, smooth dorsally, demarcated proximally by distinct dermal fold; subarticular tubercles distinct, elevated, triangular in profile, single except two most distaltubercles on Finger IV and most distal tubercle on Finger V bifid; supernumerary tubercles unequal in size, distinct, distributed evenly over ventral surfaces of foot and toes.

Skin on dorsum of body rugose with scattered, rounded tubercles of unequal size, becoming sharply pointed laterally; parotoid glands about same size as eyelids, slightly ovoid, oriented parallel to midline of body; lateral row of enlarged tubercles barely evident; dorsal surface of head smooth with few, small, rounded tubercles scattered in interspaces between cranial crests; dorsal surfaces of limbs covered with small to large, mostly pointed tubercles; all ventral surfaces rough, covered with small, conical tubercles.

Choanae small, ovoid, widely spaced; teeth and odontoids absent, but ventral surface of neopalatine appears serrate; tongue long, ovoid, about four times as long as wide, free posteriorly for about one-fourth its length; vocal slit unilateral, dextral.

Coloration of holotype.—In preservative (ethanol), dorsal areas of body and limbs mottled evenly with pale brown and dark brown markings, with a bilateral series of small, oblong cream markings dorsolaterally; top of head uniform dark brown with distinct cream interorbital bar; distinct cream middorsal stripe extending from snout to posterior end of urostyle; lateral surfaces dull brown with some dull cream supralabial spots. Ventral surfaces dull cream with indistinct pale gray markings, forming loosely reticulate pattern; dark vocal sac barely visible through gular skin.

Measurements of the holotype (in mm).—SVL 57.1, HL 20.5, HW 23.0, TL 19.9, FL 20.0, orbit diameter 8.2, tympanum diameter 4.4, supratympanic crest length 3.4, parotoid gland length 6.8, parotoid gland width 5.9.

Coloration in life.—Original field notes by R. G. Zweifel (12 June 1962) describe AMNH 69625 as "…a rather black and white looking toad, the whiteness coming from

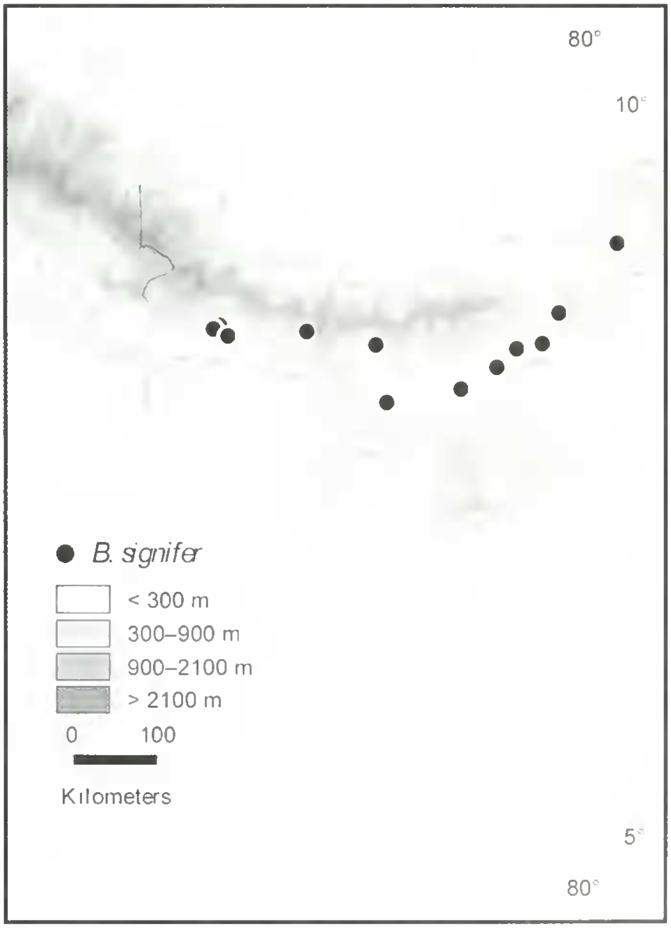

Fig. 13. Map of western Panama with dot localities for *Bufo signifer* indicating specimens examined, which represent all known localities.

the lateral stripe which begins at the parotid and runs back to the groin and by the central vertebral line. The blackness is supplied by the dorsal blotches which are almost jet-black. The ground color between the blotches is dark gray. The side below the lateral line is a mixture of black and gray. The eyelids are a stripe with grayish white and black. The interorbital area is black with a grayish white band. The ventral surfaces are mottled gray and white; there is a dark gray spot in the middle posterior gular region. The hind legs are barred very with dark gray and grayish white as are the limbs right out to the tips of the toes."

Variation.—Morphometric variation among specimens examined is summarized in Table 2. The parietal crests in males may be relatively distinct and well formed (e.g., TNHC 31343, or they may be essentially absent (e.g., TNHC 31342); this crest is always relatively distinct in females. The dorsal pattern usually consists of a contrasting array of dark brown or black blotches over a pale brown ground color, but some specimens (e.g., TNHC 46261) have a nearly uniform, dull brown dorsum. Nearly all specimens of this species bear a distinctive, highly contrasting marbled pattern on the venter; this pattern is present, but less distinct in a few specimens (e.g., TNHC 46261, USNM 297515, AMNH 69626). The middorsal cream stripe is present in all individuals, but may be incomplete (e.g., AMNH 69627).

Etymology.—The name *signifer* Latin, meaning bearing marks, refers to the ventral coloration of this species.

Reproductive biology.—The tadpole of *B. signifer* is unknown. Zweifel (personal communication) found calling males in a "weedy, shallow, muddy roadside pool" on 25 June 1962; also found in this pool were *Elachistocleis* sp. and *Leptodactylus insularum*.

Distribution and ecology.—This species is known from each of the disjunct areas of Tropical Dry Forest (Campbell and Lamar, 2004:47, color map 6) along the Pacific Coast of Panama (Fig. 13). These regions are located in the vicinity of city of David, and the Province of Veraguas eastward toward the Canal Zone.

MORPHOMETRIC ANALYSES

Overall morphometric variation for all species is summarized in Table 2. Two Principal Components Analyses were conducted: one with log-transformed data, and one using residuals of each variable regressed on SVL. These analyses produced similar results (not presented here) wherein the first PC had the greatest eigenvalue (and accounted for the majority of the variation explained) and represented an overall size axis. Despite reasonably high loadings for variables such as TYMP and PARW on the second PC, plots individual scores for each specimen did not clearly distinguish among the species. As could be expected, *Bufo coccifer* showed the most overall variation, while the smallest species (*B. pisinnus*) was somewhat distinct from the largest species (*B. ibarrai*) along the size axis (PC1). Considered together, the results of these analyses indicate that, with the exception of overall size, there has been relatively little morphometric differentiation among the species in this group.

Variable selection procedures (forward, backward, and stepwise) for LDA suggested retention of all nine variables, i.e., residuals of eight variables regressed on SVL and log-transformed SVL. The cross-validated classification-matrix from the LDA is shown in Table 3. The majority of individuals of all species were correctly classified. Individuals of *Bufo signifer* and *B. porteri* were misclassified inconsistently among all other species. *Bufo pisinnus* and *B. cycladen* had the greatest percentage (86%, 80%) of correctly classified individuals, respectively. The small size of *B. pisinnus* likely is responsible for this high degree of correct classification, but we note the 11 individuals of the quite variable species *B. coccifer* were misclassified as *B. pisinnus*; this result suggests that small *B. coccifer* are morphometrically similar to *B. pisinnus*. Similarly, the relatively large size of *B. ibarrai* likely is responsible for the relatively high percentage (79%) of correctly classified individuals of that species (and the very few individuals of other species that were identified as *B. ibarrai*). In general, these results are consistent with the results of the PCA. Despite its wide range of overall variation (Table 2), 77% of individuals of *B. coccifer* were classified correctly.

Table 3. Cross-validated classification-matrix and overall correct classification percentages (rounded to nearest integer) from Linear Discriminant Analysis based on residuals of eight morphometric variables regressed on SVL and log transformed SVL from all species in the *Bufo coccifer* Group, analysis includes only adult males. Values in boldface indicate number of individuals correctly classified.

	N	*B. coccifer*	*B. cycladen*	*B. ibarrai*	*B. pissinus*	*B. signifer*	*B. porteri*	Per cent correct classification
B. coccifer	106	**82**	4	2	11	4	3	77
B. cycladen	30	1	**24**	0	2	3	0	80
B. ibarrai	79	0	2	**62**	0	2	3	79
B. pissinus	21	1	1	0	**18**	1	0	86
B. signifer	21	0	2	1	1	**16**	1	76
B. porteri	43	3	1	1	5	1	**34**	79

Table 4. Voucher numbers and locality information for specimens of *Bufo* used in the molecular analyses. GenBank accession numbers are given for 16S and cyt-b, respectively.

Taxon	Voucher No.	Locality	GenBank No
B. ibarrai 1	UTA-ENS 10270	Honduras: Ocotepeque	AY927854, AY927861
B. ibarrai 2	UTA-JAC 19612	Guatemala: Quiche	AY927855, AY927862
B. coccifer ES	KU 290030	El Salvador: Morazán	AY927856, AY927863
B. coccifer NI	SDSNH-AFH 013	Nicaragua: Ometepe Is.	AY927857, AY927864
B. coccifer HO	USNM 547980	Honduras: Gracias A Dios	AY929301, AY929303
B. coccifer CR	TCWC 83998	Costa Rica: San José	AY929302, AY929304
B. cycladen	UTA-JRM 4607	Mexico. Guerrero	AY927858, AY927865
B. coniferus	MVZ 203775	Costa Rica: Cartago	U52800, AY008255
B. valliceps	MZFC-JRM 3868	Mexico. Veracruz	AY008211, AY008212
B. marinus	UTA A-50864	Guatemala: Zacapa	AY927860, AY927867

MOLECULAR ANALYSES

Sequences of 547 and 410 base pairs were obtained for 16S and cyt-b mtDNA genes, respectively; specimen information and GenBank Accession numbers are listed in Table 4. These sections correspond to the 4004–4556 and 16422–16818 positions for 16S and cyt b, respectively, on the mtDNA genome of *Xenopus* [Pipidae] (Roe et al., 1985). Of these 956 base pairs, 765 were constant, 191 were variable, and 85 were considered parsimony-informative characters. The partition-homogeneity test results indicated that trees from the separate genes were not significantly different from one another (P = 1.0). Parsimony analysis of the 16S region produced four trees. Parsimony analysis of the cyt-b region produced one tree that was identical the combined analysis shown in Figure 14. The differences among the 16S trees were the monophyly/paraphyly of *Bufo ibarrai*, and the relationships among *B. coccifer* (sensu stricto) samples. Parsimony analysis of all nucleotide data combined evaluated a total of 2,027,025 trees, with the best tree score of 278 steps (Fig. 15) and the worst tree score of 373 steps. The frequency distribution of trees scores had a mean of 351.60 steps (sd = 14.8; g_1 = 1.20; g_2 = 0.94). The hLRTs selected the TrN + I + G model (Tamura and Nei, 1993) as the most significant ($p < 0.01$; -lnL = - 2612.9934) with base frequencies of A = 0.3071, C = 0.2448, G = 0.1620, T = 0.2860. The substitution rate matrix was: A–G = 6.4270, C–T = 12.1788, all others were equal to 1; the proportion

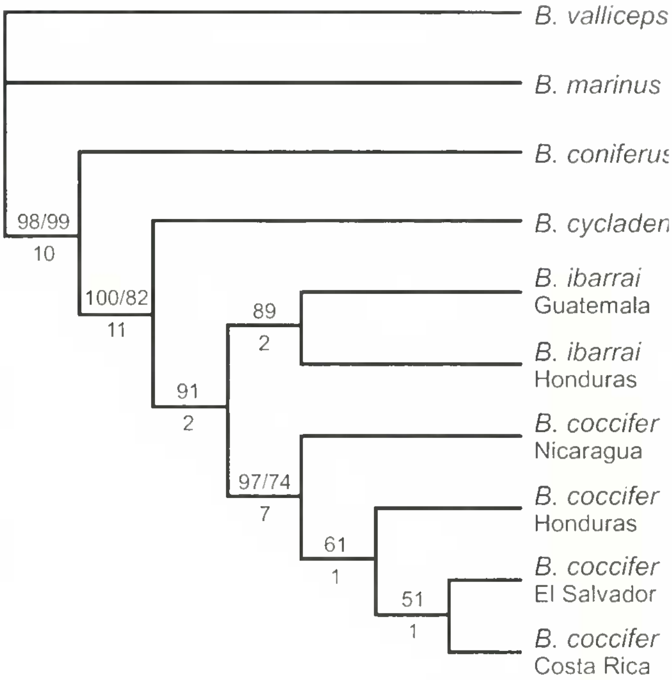

Fig. 14 Phylogenetic relationships among samples used in molecular analyses; see Table 4 for specimen information. Topology is shown from the maximum-parsimony exhaustive search. Bootstrap values greater than 50% (MP/ML) are shown for each analysis above branches and decay indices are shown below.

Table 5. Pair-wise sequence divergence of 16S and cyt b combined for specimens of *Bufo* used in the molecular analyses. Absolute distances are shown above the diagonal, and Tamura-Nei corrected distances are below the diagonal.

Taxon	1	2	3	4	5	6	7	8	9	10
1. *B. ibarrai* 1	—	6	19	17	18	19	35	70	107	113
2. *B. ibarrai* 2	0.0064	—	17	15	16	19	34	74	105	113
3. *B. coccifer* ES	0.0204	0.0182	—	4	3	8	40	72	106	115
4. *B. coccifer* NI	0.0184	0.0162	0.0043		3	10	40	72	101	112
5. *B. coccifer* HO	0.0195	0.0173	0.0032	0.0032	—	9	40	74	107	116
6. *B. coccifer* CR	0.0205	0.0205	0.0085	0.0107	0.0097	—	44	75	108	117
7. *B. cycladen*	0.0832	0.0370	0.0440	0.0445	0.0444	0.0486	—	83	108	114
8. *B. coniferus*	0.0791	0.0841	0.0816	0.0824	0.0848	0.0855	0.0950		106	124
9. *B. valliceps*	0.1261	0.1232	0.1253	0.1196	0.1277	0.1276	0.1269	0.1235		109
10. *B. marinus*	0.1325	0.1325	0.1358	0.1332	0.1383	0.1381	0.1343	0.1483	0.1292	—

of invariable sites was $I = 0.5899$ and the gamma shape parameter was $G = 0.4906$. A ML heuristic search produced a tree with a score of $\ln L = -2609.8015$ that was slightly different from the MP tree. In the ML tree (not shown), the *B. ibarrai* samples were basal to the remaining samples of *B. coccifer* (sensu lato); however the nodes in the ML analysis differing from the MP analysis were not supported in the ML bootstrap analysis. The ML bootstrap values are shown for nodes supported by more than 50% in Figure 14. Sequence divergences for the combined 16S and cyt b sequences are shown for each sample in Table 5.

The phylogenetic hypothesis generated by our data (Fig. 14) supports recognition of a monophyletic *B. coccifer* Group that contains both *B. coccifer* and *B. ibarrai* (contra Blair, 1972). Our data indicate that both *B. cycladen* and *B. ibarrai* render *B. coccifer* (sensu lato) paraphyletic. This topology, and the morphological distinctness of both *B. cycladen* and *B. ibarrai* (Mendelson, 2001; this paper), suggest that *B. coccifer* (sensu lato) represents more than one species. Our proposed taxonomy recognizes six species in this group, one of which (*B. cycladen*) was here recovered as the sister to (*B. coccifer* + *B. ibarrai*). Knowledge of the phylogenetic positions of *B. porteri*, *B. pisinnus*, and *B. signifer* must await the collection of additional samples and molecular data from these species.

LITERATURE CITED

Blair, W. F. 1963. Evolutionary relationships of North American toads of the genus *Bufo*: a progress report. Evolution 17:1–16.

Blair, W. F. 1972. *Bufo* of North and Central America. pp. 93–101 *In*: Blair, W. F. (Ed.), Evolution in the Genus *Bufo*. University of Texas Press, Austin, Texas.

Bremer, K. 1994. Branch support and tree stability. Cladistics 10:295–304

Campbell, J. A. 1999. Distribution patterns of amphibians in Middle America. Pp. 111–209 *in* W. E. Duellman (ed.), Distribution Patterns of Amphibians: A Global Perspective. Johns Hopkins University Press, Baltimore, Maryland.

Campbell, J. A., and W. E. Duellman. 2000. New species of stream-breeding hylid frogs from the northern versant of the highlands of Oaxaca, Mexico. Scientific Papers, Natural History Museum, University of Kansas 16:1–28.

Campbell, J. A., and W. W. Lamar. 2004. The venomous reptiles of the Western Hemisphere. Comstock Publishing Associate, Cornell University Press, Ithaca, New York.

Campbell, J. A., and J. P. Vannini. 1989. Distribution of amphibians and reptiles in Guatemala and Belize. Proceedings of the Western Foundation Vertebrate Zoology 4:1–21.

Cope, E. D. 1866. Fourth contribution to the herpetology of tropical America. Proceedings Academy Natural Sciences Philadelphia 18:123–130.

Cope, E. D. 1887. Catalogue of the batrachians and reptiles of Central America and Mexico. Bulletin United States National Museum 32:1–98.

Davis, W. B., and J. R. Dixon. 1965. Amphibians of the Chilpancingo Region, Mexico. Herpetologica 20:225–233.

Duellman, W. E. 1960. A distributional study of the amphibians of the Isthmus of Tehuantepec, Mexico. University of Kansas Publications Museum Natural History 13:19–72.

Duellman, W. E. 1961. The amphibians and reptiles of Michoacán, Mexico. University Kansas Publications Museum Natural History 15:1–148

Dunn, E. R. 1933. Amphibians and reptiles from El Valle de Anton, Panama. Occasional Papers Boston Society Natural History 8:65–79

Dunn, E. R., and L. C. Stuart. 1951. Comments on some recent restrictions of type localities of certain South and Central American amphibians and reptiles. Copeia 1951:55–61

Dunn, E. R., and J. T. Emlen. 1932. Reptiles and amphibians from Honduras. Proceedings Academy Natural Sciences Philadelphia 84:21–32

Flores-Villela, O. A. 1993. Herpetofauna Mexicana. Special Publications Carnegie Museum Natural History 17:1–73

Frost, D. R. (Ed.). 1985. Amphibian Species of the World: A Taxonomic and Geographic Reference. Allen Press and Association of Systematics Collections, Lawrence, Kansas.

Frost, D. R. 2003. Amphibian Species of the World: an online reference. V2.21 (15 December 2003). Electronic database available at http://research.amnh.org/herpetology/amphibia/index.html.

Frost, D. R., and D. M. Hillis. 1990. Species in concept and practice: Herpetological applications. Herpetologica 46:87–104.

Good, D. A., and D. B. Wake. 1992. Geographic variation and speciation in the Torrent salamanders of the genus *Rhyacotriton* (Caudata: Rhyacotritonidae). University of California Berkeley Publications in Zoology 126:1–91.

Gergus, E. W., B. K. Sullivan, and K. B. Malmos. 1997. Call variation in the *Bufo microscaphus* complex: implications for species boundaries and the evolution of mate recognition. Ethology 103:979–989.

Hartweg, N., and J. A. Oliver. 1940. A contribution to the herpetology of the Isthmus of Tehuantepec, IV. Miscellaneous Publications Museum of Zoology, University of Michigan 47:1–31.

Johnson, J. D. 1989. A biogeographic analysis of the herpetofauna of northwestern Nuclear Central America. Contributions in Biology and Geology Milwaukee Public Museum 76:1–66.

Johnson, J. D. 1990. Biogeographic aspects of the herpetofauna of the central depression of Chiapas, México, with comments on surrounding areas. Southwestern Naturalist 35:268–278.

Kellogg, R. 1932. Mexican tailless amphibians in the United States National Museum. Bulletin of the United States National Museum 160:1–224.

Köhler, G. 1999. The Amphibians and Reptiles of Nicaragua: A Distributional Checklist with Keys. Courier Forschungsinstitut Senckenberg 213:1–121.

Leenders, T. 2001. A Guide to the Amphibians and Reptiles of Costa Rica. Zona Tropical Publishers, Miami, Florida.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, and C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology. Copeia 1985:802–832.

Lynch, J. D., and C. M. Fugler. 1965. A survey of the frogs of Honduras. Journal of the Ohio Herpetological Society 5:5–18

Lynch, J. D., and H. M. Smith. 1966. A new toad from western Mexico. Southwestern Naturalist 11:19–23.

Masta, S. E., B. K. Sullivan, T. Lamb, and E. J. Routman. 2002. Molecular systematics, hybridization, and phylogeography of the *Bufo americanus* complex in eastern North America. Molecular Phylogenetics and Evolution 24:302–314.

McCranie, J. R., and L. D. Wilson. 2002. The Amphbians of Honduras. Society for the Study of Amphibians and Reptiles, Ithaca, New York.

McDiarmid, R. W., and M. S. Foster. 1981. Breeding habits of the toad *Bufo coccifer* in Costa Rica, with a description of the tadpole. Southwestern Naturalist 26:353–363.

Mendelson, J. R., III. 1997. A new species of *Bufo* (Anura: Bufonidae) from the Pacific Highlands of Guatemala and southern Mexico, with comments on the status of *Bufo valliceps macrocristatus*. Herpetologica 53:14–30.

Mendelson, J. R., III. 2001. A review of the Guatemalan toad *Bufo ibarrai* (Anura: Bufonidae), with distributional and taxonomic comments of *Bufo valliceps* and *Bufo coccifer*. Pp. 10–19 *in* J. D. Johnson and R. G. Webb, and O. Flores-Villela (eds.), *Mesoamerican Herpetology: Systematics, Natural History, and Conservation*. The University of Texas at El Paso, El Paso, Texas.

Mertens, R. 1952. Die Amphibien und Reptilien von El Salvador, auf Grund der Reisen von R. Mertens und A. Zilch. Abhandlen Senckenbergischen Naturforschenden Gesellschaft 487:1–83.

Meyer, J. R., and L. D. Wilson. 1971. A distributional checklist of the amphibians of Honduras. Contributions Science Natural History Museum Los Angeles County 218:1–47.

Myers, C. W., and W. E. Duellman. 1982. A new species of *Hyla* from Cerro Colorado, and other tree frog records and geographical notes from western Panama. American Museum Novitates 2752:1–25.

Mulcahy, D. G., and Mendelson, J. R., III. 2000. Phylogeography and speciation of the morphologically variable, widespread species *Bufo valliceps*, based on molecular evidence from mtDNA. Molecular Phylogenetics and Evolution 17:173–189.

Porter, K. R. 1962. Evolutionary Relationships of the *Bufo valliceps* Group in Mexico. Ph. D. Dissertation, University of Texas, Austin, Texas.

Porter, K. R. 1963. Distribution and taxonomic status of seven species of mexican *Bufo*. Herpetologica 19:229–247.

Porter, K. R. 1964. Morphological and mating call comparisons in the *Bufo valliceps* complex. The American Midland Naturalist 71:232–245.

Porter, K. R. 1965. Interspecific variation in mating call of *Bufo coccifer* Cope. The American Midland Naturalist 74:350–356.

Porter, K. R. 1966. Mating calls of six Mexican and Central American toads (genus *Bufo*). Herpetologica 22:60–67.

Porter, K. R. 1967. *Bufo cycladen* (Bufonidae): a case of *nomen dubium*. Southwestern Naturalist 12:200–201.

Porter, K. R., and W. F. Porter. 1967. Venom comparisons and relationships of twenty species of New World toads (genus *Bufo*). Copeia 1967:298–307.

Posada, D., and K. A. Crandall. 1998. Modeltest. testing the model of DNA substitution. Bioinformatics 14: 817–818.

Rand, A. S. 1957. Notes on amphibians and reptiles from El Salvador. Fieldiana Zoology 34:505–534.

Roe, B. A., D. P. Ma, R. K. Wilson, and J. F. H. Wong. 1985. The complete sequence of the *Xenopus laevis* mitochondrial genome Journal Biological Chemistry 260:9759–9774.

Rzedowski, J. 1994. Vegetación de México. Limusa Noriega Editores, Mexico City, Mexico.

SAS software, Version 8 of the SAS System for Windows. 1999–2000. SAS Institute Inc. SAS and all other SAS Institute Inc. product or service names are registered trademarks or trademarks of SAS Institute Inc., Cary, North Carolina.

Savage, J. M. 1974. Type localities for species of amphibians and reptiles described from Costa Rica. Revista de Biologia Tropical 22:71–122.

Savage, J. M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas. University of Chicago Press, Chicago, Illinois.

Savage, J. M., and W. R. Heyer. 1967. Variation and distribution in the frog genus *Phyllomedusa* in Costa Rica, Central America. Beitrage Zur Neotropischen Fauna 5:111–131.

Savage, J. M. and W. R. Heyer. 1997. Digital webbing formulae for anurans: a refinement. Herpetological Review 28:131.

Savage, J. M., and J. D. Villa. 1986. Introduction to the herpetofauna of Costa Rica. Contributions to Herpetology 5, Society for the Study of Amphibians and Reptiles, Oxford, Ohio.

Schmidt, K. P., and L. C. Stuart. 1941. The herpetological fauna of the Salama Basin, Baja Verapaz, Guatemala. Zoological Series of the Field Museum of Natural History 24:233–247.

Smith, H. M., and E. H. Taylor. 1948. An annotated checklist and key to the amphibia of Mexico. Bulletin United States National Museum 194:1–118.

Sorenson, M.D. 1996. TreeRot. University of Michigan, Ann Arbor.

Stuart, L. C. 1954a. A description of a subhumid corridor across northern Central America, with comments on its herpetofaunal indicators. Contributions Laboratory Vertebrate Zoology, University of Michigan 65:1–26.

Stuart, L. C. 1954b. Descriptions of some new amphibians and reptiles from Guatemala. Proceedings of the Biological Society Washington 67:159–178.

Stuart, L. C. 1963. A checklist of the herpetofauna of Guatemala. Miscellaneous Publications, Museum of Zoology, University of Michigan 122:1–150.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and other methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.

Tamura K., and M. Nei. 1993. Estimation of the number of nucleotide substitutions in the control region of mitochondrial DNA and chimpanzees. Molecular Biology and Evolution 10:512–526.

Taylor, E. H. 1952. A review of the frogs and toads of Costa Rica. University of Kansas Science Bulletin XXXV:577–942.

Tyler, M. J., T. Burton, and A. M. Bauer. 2001. Parotid or parotoid: on the nomenclature of an amphibian skin gland. Herpetological Review 32:79–81.

Villa, J. 1972. Anfibios de Nicaragua. Instituto Geográfica Nacional and Banco Central de Nicaragua.

Villa, J. 1983. Nicaraguan fishes, amphibians, and reptiles: a checklist and bibliography. Escuela de Ecología y Recursos Naturales, Universidad Centroamericana, Managua, Nicaragua.

Villa, J., L. D. Wilson, and J. D. Johnson. 1988. Middle American Herpetology: A Bibliographic Checklist. University of Missouri Press, Columbia, Missouri.

Werner, F. 1896. Beiträge zur kenntniss der reptilien und batrachier von Centralamerika und Chile. Verhandl. k.k. Zool.-Bot. Gesell. Wien 46:1–24.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. Systematic Zoology 27:17–26.

Zweifel, R. G. 1965. Distribution and mating calls of the Panamanian toads, *Bufo coccifer* and *B. granulosus*. Copeia 1965:108–110.

APPENDIX

Specimens examined

Note that data presented here has been taken verbatim from museum catalogs and tags. We have not attempted to correct various spellings, nor to alter original estimates of distance and elevation. We do not consider it reasonable to re-estimate primary locality data.

Bufo coccifer: **Costa Rica:** Alajuela: Río Grande (LACM 59432). Puntarenas: 1.5 km W Barranca, 20 m (KU 65381); 4 km WNW Esparta, 45 m (KU 65397–90, 65393, 65397–98, 65400, 65404–05, 65414). San José: Guadalupe, 1190 m (KU 65379); Escazú, 1100 m (KU 65380). **Guatemala:** Chiquimula: above headquarters of Finca San José, ca. 6.0 km SE Concepción Las Minas (UTA A-38119); Finca San José, ca. 6.0 km SE Concepción Las Minas on rd to Las Presas (UTA A-38123–26); Concepción Las Minas, Valle Arriba (UTA A-47566); 2.6 mi N intersection of CA-12 and CA-10 (UTA A-38120–21); Jalapa: Volcán Jumay (UTA A-47591). Retalhuleu: 3.2 km N Champerico (UTA A-25814–23); 3.7 km N Champerico (UTA A-29021–25). Santa Rosa: El Oratorio, 3.0 km E CA-8 (UTA A-38143). **El Salvador:** Chalatenango: 16.5 km WNW Chalatengo (KU 184659–62); 10 km NE La Palma, Canton Las Pilas (KU 184663–69). Cuscatlan: Tenancingo, Río Quezalapa (KU 184572–73); 7 km W Cojutepeque, 2900 ft (KU 97495); 8 km W Cojutepeque, 2850 ft (KU 97499–504); Cojutepeque, 3220 ft (KU 97505–09); 0.5 km SE Cojutepeque, 2520 ft (KU 97510–11); 2 km E Cojutepeque, 3250 ft (KU 97496). La Libertad: 10 mi NW Santa Tecla (KU 41411–29); 5 mi W Colón (KU 97473–86); 5.4 mi W La Libertad, 680 ft (KU 97487–92); San Bartolo, 11 km E San Salvador, 2595 ft (KU 97493). La Union: Laguna Olomega (KU 184574). Morazan: 12 km NE Perquin, Canton, El Zancudo (KU 184578–609); grounds of Hotel Perquin Lenca, Perquin, 1150 m (KU 290030). San Salvador: 1 mi NW San Salvador (KU 42613–24); Instituto Tropical (KU 61871–74); 16 km E San Salvador, 2880 ft (KU 97494); 3 km SE Ilopango, Canton Asino (KU 184575–77, 184670–74); San Salvador, Cuidad Universitaria (KU 184612–58, 184715–16). Santa Ana: Rancho San José, 800 m (KU 65372). San Vicente: 1 km E El Carmen (12 km E Cojutepeque), 2620 ft (KU 97497); 6.5 km E El Carmen (17.5 km E Cojutepeque), 2700 ft (KU 97498). **Honduras:** Choluteca: 6.8 mi S Prespire, 380 ft (TNHC 31461); Choluteca (USNM 167195); 1.5 km NW Choluteca, 170 m (KU 65375–76); San Francisco de Colón, 1130 m (KU 65374). El Paraiso: 4.4 mi SW Santa María, 1960 ft (KU 97512–13). Francisco Morazan: 10.3 mi S La Vente, 530 ft (TNHC 31454); vic. of Tegucigalpa (LSUMZ 24133–34). Gracias a Dios: Rus Rus, 60 m (USNM 547977, 547980); Mocorón (UTA-CJF 1883–84). Olancho: 1 km NW Catacamas (LACM 47973–74, 21584–89); Catacamas, 460 m (KU 194214); ca. Dulce Nombre de Culmi, 600 m (KU 194213). Valle: 1 mi E Goascoran (LACM 47975–77); 3 mi E Goascoran (LACM 47978–82); 5.2 mi SE Jicaro Galán, 250 ft (TNHC 31456, 31459). **México:** Chiapas: road from Tapachula to Puerto Madero. Oaxaca: 0.1 mi S jct 185 & 190, on 185 (LACM 38160–61); Juchitán (USNM 51175); 4 mi S Juchitan, 120 ft (KU 97434–42,); 1.5 mi N Juchitán, 120 ft (KU 97443); 3 mi N Juchitan, 120 ft (KU 97444–47); 0.5 mi S Juchitán, 140 ft (KU 97448–50); 5 mi N Juchitan, 110 ft (KU 97451–62); Juchitán, 9 mi E jct hwys 190 and 185 (TNHC 30968); Hwy 185, 14.2 mi N jct Hwy 190 (TNHC 53682, 53684); 1 mi NW Zanatepec (TNHC 31338); 20 mi W Zanatepec (TNHC 27161); 3 mi W Zanatepec (TNHC 27165); 10 mi W Zanatepec (TNHC 27292); Zanatepec (TNHC 27300); 17 mi E Tehuantepec (TNHC 27282, 27284, 27286, 27288, 27290, 27305); 40 mi E Juchitan (TNHC 27291); edge of Tepantepec (TNHC 27293, 27295, 29297). **Nicaragua:** Granada: shore of Lago de Nicaragua, ca 2 mi from Granada (LACM 67585). Managua: Managua, S shores of Lake Managua (LACM 28165–69); Los Robles (LACM 37957–58, KU 173951–53, 173955–56); 2–5 km S Tipitapa (KU 173958). Rivas: Nandaime, 400 ft (KU 97547). Zelaya Norte: Leicus Creek at La Tronquera (NIPCO Lumber Plant), 56 mi NW Puerto Cabeza (LACM 145808); Shlma Sia, 16 km SE Waspam, Comarca de El Cabo (LACM 145813).

Bufo cycladen: **México:** Guerrero: near Palo Blanco (FMNH 99682, 99686, UIMNH 24834–38); Xaltianguis (UIMNH 24833); Agua del Obispo, KM 350–351 (UIMNH 24839), Agua del Obispo, KM 357 (UIMNH 24840); 4 km beyond Agua del Obispo (UIMNH 24841–45); near Agua del Obispo (FMNH 99684–85, 99687–90, 105394, 107984–91, USNM 11548283); Agua del Obispo (UIMNH 24846, 24848–50, 24875–76, 57143); Agua del Obispo, 980 m (KU 86672–73); Agua del Obispo, 2900 ft (UMMZ 115357 [6 specimens]). Oaxaca: 3 mi S Putla (UIMNH 57144–51).

Bufo ibarrai: **Guatemala:** Baja Verapaz: Chilasco (UTA A-47567–69); circa 5 km S Chilasco, 1800 m (MVZ 143379); 8 km ESE Chilasco, Finca Miranda, 6500 ft [1981 m] (MVZ 150931); 50.2 km NW El Rancho (UTA A-5016); CA-14, 29.0 mi [46.7 km] NW El Rancho (UTA A-5049); CA-14, 50.2 km NW El Rancho (UTA A-5015); 4.8 mi [7.7 km] SSE Purulhá, Plantación Santa Teresa (UTA A-7417); 9.1 mi [14.6 km] W Salamá (by road to Purulhá) (UTA A-7432); 2.4 mi [3.9 km] W Purulhá (UTA A-8502–07); 3.5 mi [5.6 km] W Purulhá (UTA A-30495 larvae); 3.2 km WNW Purulhá (UTA A-17117–18); 3.5 km W western Purulhá turnoff (UTA A-17242–17244); 2.7 km W western Purulhá turnoff (UTA A-17245); 3.8 km W Purulhá, 1536 m (KU 186288–303); 7.7 km SE Purulhá, 1615 m (KU 186304); 3.8 km W Purulha, 1524 m (KU 190067); 4.2 km W Purulhá, 1524 m (KU 190068–70); 3.4 km W Purulhá, 1524 m (KU 190071); 2.0 km W Purulhá (UTA A-38145–49); Hwy CA-17 between El Rancho and Cobán, km 126 (UTA A-43977–78); 1 km S San Geronimo (UMMZ 84083). El Quiche: Joyabaj (KU 186305); La Primavera, between Sacapulas and Santa Cruz Quiche, 6600 ft [2012 m] (UMMZ 126307). Guatemala: Amatitlan (UTA A-38144); 11.2 km SW Guatemala City, 4600 ft [1402 m] (KU 97595–609); 21 km SW Guatemala City, 4480 ft [1366 m] (KU 97610–19], Guatemala City, zone 10, 4820 ft [1469 m] (TNHC 31384, 31387, 31390, 31392, 31395, 31399, 31401–02, 31405, 31408, 31416–20, 31422, 31426, 31430–33); Guatemala City, between zone 5 and zone 15, km 2.5 (UTA A-25824); E side Guatemala City, zone 16, 1 km N Vista Hermosa III on road to Santa Rosita (UTA A-25825–32); Santa Catarina Pinula, San Miguel Buena Vista, 1700 m (UTA A-43951, UTA A-47570–74); Guatemala City, zone 15, Vista Hermosa III, 1510 m (UTA A-28959–60); Parque San Jorge Muxbal, 1850 m (UTA A-32993). Huehuetenango: Aguacatán (UMMZ 120046); 2 km NE Aguacatán, 1640 m (UMMZ 120047–48); 2.8 km E Aguacatán, 1600 m (KU 58412–13); Huehuetenango, patio of Casa Maryknoll (UMMZ 124382); 22 km SSW Huehuetenango (KU 116959); 3 km W Huehuetenango, 6100 ft [1859 m] (TNHC 29452–57); at La Libertad, 1700 m (MVZ 143343–57); San Pedro Necta (UMMZ 130059 larvae); circa 1 km E San Pedro Necta, 1615 m (UMMZ 119352). Jalapa: Jalapa (TNHC 33666–72); 8.5 km NW Jalapa (TNHC 31442); 7.5 km WSW Jalapa, on road to Miramundo (UTA A-39114 larvae); Jalapa–Miramundo rd, at km 101 (UTA A-38118); Falda Oeste Volcan Jumay (UTA A-47565); 1.6 mi [2.5 km] NE El Mojón (UTA A-38127–40); 0.7 mi [1.1 km] NE El Mojón (UTA A-38141); Aserradero San Lorenzo (circa 12 air km NNE Jalapa), 1725 m (UMMZ 108000, 106806 [10 specimens], 106807 [3 specimens]. Progreso: Finca Bucaral (UMMZ 106808, 139516 larvae). Sacatepequez: 3 km W Dueñas (TNHC 31378); 1.3 mi [4.4 km] W Finca San Rafael Urias at Dueñas (TNHC 31344, 31379–80); San Antonio (CAS 70826–27); Volcan Agua (CAS 70719–825). **Honduras:** Intibuca: water supply area for La Esperanza (LACM 45247–48) 1.5 mi NE La Esperanza (LACM 47992–96); 1 mi NE La Esperanza (LACM 47998); La Esperanza (LACM 47998–48004); 25. 7 km NW La Esperanza, 1340 m (USNM 523689–93); 18.1 km NW La Esperanza, 1740 m (USNM 523694–96), 8.7 km NW La Esperanza, 1540 m (USNM 523697); Zacate Blanco, 2020 m (KU 194220–21); ca Miguelito, 60.3 km SE Gracias (Depto. Lempira), 1310 m (KU 209250, 209253). Lempira: Erandique (LSUMZ 46432, 49738); above Villa Verde, 1280 m (KU 209240). Ocotepeque: 12.5 mi E Nueva Ocotepeque (LACM 47983–85); 6.5 mi E Nueva Ocotepeque (LACM 47986–91); "14°29.48'N, 88°46.83'W" (UTA A-52960, 53662); Belen Gualcho, 1470 m (KU 194208); El Chaguiton, 1870 m (KU 194209–12; USNM 523712–13); El Volcan, 1760 m (USNM 523714–18).

Bufo pisinnus: **Mexico:** Michoacan: 9 mi on rd between Río Marquez and Cuatro Caminos (KU 62237–41); 1–6 mi S Cuatros Caminos (LACM 37092–96); 7 mi E Apatzingan, 1100 ft (UMMZ 115355, 112794 [6 specimens]); 1 mi E Apatzingán, 1100 ft (UMMZ 115354 [2 specimens]); 3 mi S Lombardia (UMMZ 121578); 6.2 mi E Apatzingán, 1100 ft (UMMZ 115353 [15 specimens], 233723).

Bufo porteri: **Honduras:** Comayagua: 10.9 mi NW Siguatepeque (TNHC 31444); 6.9 mi NW Siguatepeque, 3820 ft (TNHC 31462, 31466); 7.5 mi NW Siguatepeque, 3500 ft (KU 97527); 8.8 mi NW Siguatepeque (TNHC 31468); Siguatepeque, 3500 ft (FMNH 4612–13); 9.8 km SW Siguatepeque, 1700 m (USNM 523683); 9.8 km SW Siguatepeque, 1950 m (USNM 523684);Montana de Comayagua above Río Negro, 1530 m (KU 209247). Francisco Morazan: Morizán, 21.4 km SE San Antonio, 4820 ft (TNHC 31446, 31450, 31452, 31454); 17.1 mi S Tegucigalpa, 4900 ft (TNHC 31455); Cerro Cantagallo, 1840 m (USNM 523686); Monte Crudo, nr EAP, 6000 ft (AMNH 54757); La Montanuela, above Table Grande, above EAP (AMNH 54758–59); Uyuca, above EAP, 5800 ft (AMNH 54760); Cerro Uyuca, 1900 m (KU 209254); Uyuca, above EAP, above Tatumbla, ca. 5300 ft (AMNH 54761); slopes of Uyuca, 4500–5000 ft (AMNH 54822); 5.5 mi SW Valle de Angeles (LACM 47970–71); 4.7 mi SW San Juancito (LACM 47972); 8.6 mi NW Comayaguela (LACM 59426–31); 5 km W Zambrano, 1635 m (KU 65373); Cerro Uyuca (LSUMZ 45433, 45439–40, 45456, 46400, 46427, 49737); Cerro La Tigra (LSUMZ 45436, 45444, 45452); Cerro La Tigra, 1840 m (KU 194215–19, 209249); 6 mi NE Escuela Panamericana, Cerro Uyuca, 5400 ft (KU 97514–18); 6 mi NE Escuela Panamericana, Cerro Uyuca, 5200 ft (KU 97519–26); W slope Cerro Uyuca, 1750 m (KU 103220); W slope Cerro Uyuca, 1650 m (KU 103221); Parque Nacional La Tigra, above San Juancito, 2100 m (KU 192294); El Hatillo (LSUMZ 45438, 45441, 45446, 46418; LACM 72072). La Paz: Marcala (LSUMZ 46396–98, 46401, 46405, 46407, 46412–14, 46420, 46422–24, 46426, 46428, 46431, 46434–35, 46442, 46445, 46448–51, 46453–55); Santa Elena, 1750 m (KU 194222); Sierra de Montecillos, about Tutule, 1750 m (KU 209244).

Bufo signifer: **Panama** Canal Zone: no further data (TNHC 46261). Chiriqui: Cerro Colorado, Escopeta Camp, ca 23 km NNE San Felix, 900 m (USNM 297511–15, 297517–21); Cerro Bollo, 3.5 km E of Escopeta Camp, 1800–1850 m (USNM 297516, 297522); 7 mi N and 2 mi W David (AMNH 69626); 7 mi E Concepción (AMNH 69627); Cerro Bollo, 3.5 km E Escopeta Camp, ca. 1800 m (USNM 297522); 2.5 mi NE David (TNHC 31340–43). Cocle: Agua Dulce (UMMZ 167438); El Valle, 2000 ft (ANSP 23418–19); El Valle de Anton (AMNH 59634, 59637); 16 km S and 9 km W Penonome, 30 m (KU 115359–61); 3.2 km W Aguadulce, 15 m (KU 115362). Herrera: 3 mi SW Pan-Am Hwy on rd past Potuga (UMMZ 167373); Jacinto, 2250 ft (ANSP 22341–44); Veraguas: 14 km NE Sona, 75 m (KU 95432).